

**ACTA  
SOCIETATIS  
ZOOLOGICAE  
BOHEMICAЕ**

ACTA SOCIETATIS ZOOLOGICAE BOHEMICAE <sup>1)</sup>

*Acta Soc. Zool. Bohem.* Vol. 59, No. 1-2

issued 1995 June 22

ISSN 0862-5247

47678

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Published and distributed by the Czech Zoological Society. Orders should be sent to the Czech Zoological Society, Viničná 7, CZ 128 00 Praha 2, Czech Republic. Printed by the Čihák tisk, Štěrboholska 21, CZ 102 00 Praha 10, Czech Republic.

Annual subscription (Volume 59, 1995, 4 issues)

Institutional subscription	Europe	USD 80.00
Other countries		USD 90.00
Private subscription	Europe	USD 40.00
Other countries		USD 50.00
Czech Republic		Kč 120,- (excl. postage)

This issue was supported by the Český literární fond (Czech Literary Foundation)

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<sup>1)</sup> A direct continuation of

(i) Vol. 1 (1927-1932) Zpráva o činnosti československé zoologické Společnosti za leta 1927-1932

(ii) Vol. 2-53 (1933-1989) Vestník československé Společnosti zoologické (*Věst Čs. Společ. Zool.*)

(iii) Vol. 54-56 (1990-1992) Acta Societatis Zoologicae Bohemoslovacae (*Acta Soc. Zool. Bohemoslov.*)

**Testate amoebae (Protozoa: Rhizopoda) from a primary mountain rain forest in the  
Tam-Dao region (Vietnam)**

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Received January 13, 1995; accepted February 9, 1995  
Published June 22, 1995

**Taxonomy, new taxa, ecology, faunistic, testacea, tropical rain forest, soil, Vietnam**

**Abstract.** From 17 samples of soil and leaf litter from a primary mountain rain forest in the Tam-Dao area 126 species, varieties and forms of testate amoebae were determined. The variety *Cyclopyxis quadratus* var. *grandis* var. n. and the species *Hyalosphenia tamdaoensis* sp. n. and *Trinema staryi* sp. n. are new for the science. All of the found species are new for the fauna of Vietnam. 34 species and varieties were first found in Asia. Relative similarity of testacean communities on the studied area in general and heterogeneity on the single microhabitats were determined on the basis of Sørensen's index of faunistic similarity at the species and genera levels.

**INTRODUCTION**

This paper is result of a study of testate amoebae fauna in soil and litter samples from a primary mountain rain (foggy) forest in the Tam-Dao region. These samples were collected by Dr J. Stary (Institute of Soil Biology AS CR) during his study stay in Vietnam in October 1988.

This paper is the first contribution what engage with soil testate amoebae fauna from this country. Golemansky (1979) studied the marine supralittoral psammal testacean fauna of the sand beaches in the southern part of Vietnam (Chinese Sea coast).

From the south-eastern Asia there are many works which supply the basic knowledge of the testate amoebae fauna from this area:

- Borneo - Hoogenraad & de Groot (1942);
- China - Bartoš (1963a), Fielde (1887), Lammerman (1907), Tai (1931), Wang (1925), Wang & Nie (1934), Zanyin Gaw (1941);
- India - Carter (1864, 1865), Naidu (1966), Nair (1968), Nair & Mukherje (1968), Rao (1928);
- Japan - Couteaux (1978), Edmonson & Kingman (1913, 1914), Hada (1969), Sudzuki (1971a, b, 1978a, b);
- Java - Bartoš (1963b), Hoogenraad & de Groot (1940, 1942), van Oye (1922, 1949);
- Malaysia - Chardez (1979), Sudzuki (1973);
- Nepal - Bhatia (1930), Bonnet (1977), Laminger (1972), Penard (1907);
- Papua - New Guinea - Bonnet (1980b), Daday (1901);
- Philippines - Bonnet (1980a);
- Singapore - Ghosh (1928);
- Sri Lanka - Daday (1898);
- Sumatra - Brues (1939), Dammermann (1948), Green et al. (1976), Harnisch (1933, 1951), Heinis (1928);
- Thailand - Bonnet (1981).

The greater part of these works deal with testate amoebae fauna from mosses and waters. Only a few papers describe the soil testate amoebae communities (e.g. Bonnet 1980, 1981; Laminger 1972).

The presented paper is the first work about the soil testate amoebae fauna from Vietnam, but also a contribution to the knowledge of the soil testate amoebae from the tropical south-eastern Asia.

#### DESCRIPTION OF THE STUDIED AREA

The studied samples were collected in the course of October, 1988 in the environs of the Tum-Dao city in the north mountain area of Vietnam (Fig. 1). The investigated locality lies ca 90 kilometers north from Hanoi ( $106^{\circ} - 106^{\circ}30' \text{ E}$ ,  $21^{\circ}31' - 22^{\circ} \text{ N}$ ). The samples were collected in the altitude ca 1200 a.s.l. Mean year value of the precipitation is 2000 mm, mean year value of the temperature is  $20^{\circ}\text{C}$ . This locality is a undisturbed primary mountain rain (foggy) forest on the slopes of limestone mountains. Floristically and faunistically it is here the boundary between the Palearctic and Indomalaysian areas and the environs of the Tum-Dao city is characterized by a mixture of elements of both geographical areas (it is known for instance by Oribaid mites and Lepidopters).



Fig. 1 Sketch-map of the study area.

The samples were collected in the primary mountain rain forest on the following sample sites:

- 182 - very moist, disintegrated wood matter, mixed with mineral particles and litter, high content of iron and manganese salts, dark rusty brown colour
- 183 - upper undisturbed leaf litter layer with mineral particles and arthropodic moder
- 184 - partial disintegrated leaf litter mixed with arthropodic moder
- 185 - partial disintegrated leaf litter mixed with mineral particles, dark rusty brown colour.
- 186 - disintegrated, very moist leaf litter mixed with arthropodic moder and mineral particles.
- 188 - humic soil horizon with mineral grains
- 189 - very disintegrated leaf litter
- 190 - very disintegrated wood matter mixed with excrements of arthropods and mineral particles
- 191 - disintegrated wood matter mixed with rusty brown ferric soil



- 192 - fermentation layer of humic soil horizon, a mixture of disintegrated leaves, twigs and mineral particles  
 193 - upper litter layer, undisintegrated leaves, petioles and rind  
 195 - very disintegrated leaf litter mixed with excrements of arthropods and with dark rusty brown mineral particles  
 196 - arthropodic moder, dark brown  
 197 - pure arthropodic moder  
 198 - undisintegrated leaf litter  
 199 - disintegrated leaf litter mixed with arthropodic moder  
 200 - undisintegrated leaf litter with rusty brown mineral particles

All of these samples were removed on the relative small area in a primary mountain rain forest and they render the variability in this relatively homogenous ecosystem

## RESULTS

### List of determined species

The numbers behind the scientific names of species are the numbers of sample sites. Numbers in brackets marked the frequency of single species. All species found are new for the fauna of Vietnam. The symbol "\*" marks a new species for Asia, the symbol "\*\*" new for science.

- Arcella arenaria* Greoff, 1866 - 197 (5 9)  
 \* *Arcella costata* var. *angulosa* (Perty) Playfair, 1918 - 196 (5 9)  
 \* *Arcella polypora* Penard, 1890 - 189 (5 9)  
*Arcella vulgaris* Ehrenberg, 1832 - 183, 190, 192, 195, 196, 200 (35 3)
- Assulina muscorum* Greoff, 1866 - 182, 183, 189, 190, 193, 196, 200 (41 2)  
 \* *Assulina muscorum* var. *denticulata* Chardez, 1964 - 183, 196 (11 8)  
 \* *Assulina muscorum* var. *stenostoma* Schonhorn, 1964 - 196 (5 9)  
*Assulina tenuicolum* (Ehrenberg) Leidy, 1879 - 185 (5 9)
- Centropyxis aculeata* (Ehrenberg) Stein, 1857 - 191, 193, 195, (17 6)  
 \* *Centropyxis aculeata* var. *oblonga* Deflandre, 1929 - 186 (5 9)  
*Centropyxis aerophila* Deflandre, 1929 - 189, 192 (11 8)  
*Centropyxis aerophila* var. *microstoma* Declotire - 196, 197, 198 (17 6)  
*Centropyxis aerophila* var. *minuta* Chardez, 1964 - 190, 196, 197, 199 (23 5)  
*Centropyxis aerophila* var. *sphagnicola* Deflandre, 1929 - 199 (5 9)  
*Centropyxis castis* (Wallich) Deflandre, 1929 - 186 (5 9)  
 \* *Centropyxis celsis* var. *minima* van Oye, 1958 - 190 (5 9)  
*Centropyxis constricta* var. *minima* Declotire, 1954 - 195 (5 9)  
 \* *Centropyxis cornuta* Declotire, 1961 - 183 (5 9)  
*Centropyxis deflandriana* Bonnet, 1959 - 184, 185, 193, 195, 196, 197, 198, 199, 200 (52 9)  
*Centropyxis ecoris* (Ehrenberg) Leidy, 1879 - 183 (5 9)  
*Centropyxis elongata* (Penard) Thomas, 1959 - 184, 190 (11 8)  
*Centropyxis lauddeflandriana* Bonnet, 1979 - 186 (5 9)  
*Centropyxis orbicularis* Deflandre, 1929 - 197 (5 9)  
 \* *Centropyxis ovalis* Declotire, 1974 - 184 (5 9)  
*Centropyxis parviflandriana* (Bonnet) Bonnet, 1979 - 183, 185, 188, 189, 191, 197, 199, 200 (47 1)  
*Centropyxis platystoma* (Penard) Deflandre, 1929 - 184 (5 9)  
*Centropyxis protecta* Baroš, 1963 - 190 (5 9)  
*Centropyxis stenodeflandriana* Bonnet, 1979 - 183, 184, 185, 186, 190, 193, 198, 199 (47 1)
- \* *Corythion aerophila* Declotire, 1950 - 183 (5 9)  
*Corythion dubium* Taránek, 1881 - 183, 184, 185, 186, 188, 189, 191, 198, 200 (52 9)  
*Corythion pulchellum* Penard, 1890 - 190, 197, 200 (17 6)

- Cyclopyxis ambigua* Bonnet & Thomas, 1960 - 185, 196 (11 8)  
*Cyclopyxis euryzona* Deflandre, 1929 - 193, 197 (11 8)  
 \* *Cyclopyxis euryzona* var *grandis* Declaire - 190 (5 9)  
*Cyclopyxis humilis* Bonnet, 1962 - 197 (5 9)  
*Cyclopyxis kahli* Deflandre, 1929 - 183, 191, 200 (17 6)  
*Cyclopyxis kahli* var *cyclostoma* Bonnet & Thomas, 1960 - 197, 199 (11 8)  
 \*\* *Cyclopyxis quadratus* var *grandis* var n - 189 (5 9)  
*Cyclopyxis stephanostoma* Bonnet, 1980 - 195 (5 9)  
*Cyclopyxis trilobata* Bartoš, 1963 - 185, 189, 192, 193 (23 5)
- Deharvengia papuensis* Bonnet, 1979 - 199 (5 9)
- Diffugia lucida* Penard, 1890 - 197 (5 9)  
 \* *Diffugia minutissima* Penard, 1904 - 184 (5 9)
- Diffugiella crenulata* (Playfair) Grospletsch, 1964 - 186 (5 9)  
*Diffugiella crenulata* var *globosa* (Playfair) Grospletsch, 1964 - 184 (5 9)  
 \* *Diffugiella horrida* Schonborn, 1965 - 182 (5 9)  
 \* *Diffugiella oviformis* (Penard) Bonnet & Thomas, 1955 - 182 (5 9)  
 \* *Diffugiella oviformis* var *fusca* (Penard) Bonnet & Thomas, 1955 - 184 (5 9)  
 \* *Diffugiella pusilla* (Playfair) Grospletsch, 1964 - 192 (5 9)
- \* *Euglyphis acanthophara* var *equus* Declaire, 1956 - 196 (5 9)  
*Euglyphis bryophila* Brown, 1911 - 195 (5 9)  
*Euglyphis citata* (Ehrenberg) Leidy, 1878 - 188 (5 9)  
*Euglyphis citata* var *glabra* Wailes, 1915 - 197, 199 (11 8)  
*Euglyphis compressa* var *glabra* Wailes, 1915 - 192 (5 9)  
*Euglyphis cristata* Leidy, 1879 - 183, 184, 185, 188, 189, 190, 192, 193, 195, 196, 197, 198, 199, 200 (82 4)  
*Euglyphis cristata* for *decora* (Ehrenberg) Jung, 1942 - 183, 191, 193 (17 6)  
 \* *Euglyphis cristata* var *lanceolata* Playfair, 1917 - 192, 196, 197, 199 (23 5)  
*Euglyphis filifera* Penard, 1890 - 192 (5 9)  
 \* *Euglyphis filifera* var *pyriformis* Wailes, 1915 - 185, 195, 196, 197 (23 5)  
*Euglyphis laevis* (Ehrenberg) Peity, 1849 - 183, 184, 185, 186, 188, 189, 190, 192, 196, 197, 198, 199, 200 (76 5)  
*Euglyphis polylepis* (Bonnet) Bonnet & Thomas, 1960 - 192 (5 9)  
*Euglyphis rotunda* Wailes & Penard, 1911 - 183, 184, 189, 190, 191, 196, 197, 198, 199 (52 9)  
*Euglyphis rotunda* var *minor* Wailes, 1915 - 186, 193, 195 (17 6)  
 \* *Euglyphis rotunda* var *obliqua* Declaire, 1956 - 185, 196 (11 8)  
*Euglyphis strigosa* (Ehrenberg) Leidy, 1879 - 185, 186, 188, 191, 193, 196, 197, 200 (47 1)  
*Euglyphis strigosa* var *glabra* Wailes, 1915 - 183, 196, 200 (17 6)  
 \* *Euglyphis strigosa* var *heterospina* (Penard) Wailes & Penard, 1911 - 184, 185, 191, 200 (23 5)  
*Euglyphis tuberculata* Dujardin, 1841 - 184, 185, 189, 190, 192, 196, 197, 198, 200 (52 9)  
 \* *Euglyphis tuberculata* var *minor* for *subcylindrica* Declaire, 1955 - 197 (5 9)  
*Euglyphis tuberculata* var *subcylindrica* (Playfair) Declaire, 1962 - 185, 198 (11 8)
- \* *Heleopera alvina* Coutaux & Chardez, 1981 - 200 (5 9)  
 \* *Heleopera minuta* Schonborn, 1965 - 185, 188, 189, 190, 192, 196, 198, 199, 200 (52 9)  
*Heleopera penard* Bonnet & Thomas, 1955 - 186, 195, 196 (17 6)  
*Heleopera petricola* Leidy, 1879 - 183, 186, 190, 192, 196, 199, 200 (41 2)  
*Heleopera petricola* var *ameihsena* Penard, 1902 - 183, 184, 192, 195, 196, 197, 199 (41 2)  
*Heleopera picta* Leidy, 1879 - 186, 188, 199, 200 (23 5)  
*Heleopera sylvatica* Penard, 1890 - 184, 185, 193, 196, 197, 200 (35 3)
- Hyalosphenia insecta* Harnisch, 1938 - 196 (5 9)  
*Hyalosphenia papilio* (Leidy) Leidy, 1879 - 195 (5 9)  
 \* *Hyalosphenia schoutedeni* van Oye, 1956 - 198 (5 9)  
 \* *Hyalosphenia schoutedeni* var *rotundata* van Oye, 1958 - 182 (5 9)

*Hyalosphenia subflava* Cash, 1909 - 182, 186, 188, 198, 200 (29 4)

\*\* *Hyalosphenia tumidocensus* sp. n. - 196 (5 9)

*Nebela bohémica* Taránek, 1882 - 183, 195 (11 8)

*Nebela caudata* Leidy, 1879 - 185 (5 9)

*Nebela collaris* (Ehrenberg) Leidy, 1879 - 183, 198 (11 8)

*Nebela densistoma* Penard, 1890 - 185, 189 (11 8)

*Nebela lageniformis* Penard, 1890 - 183, 195, 196, 199 (23 5)

*Nebela militaris* Penard, 1890 - 195, 197, 200 (17 6)

*Nebela penardiana* Deflandre, 1936 - 183, 186, 193, 195 (23 5)

*Nebela tincta* (Leidy) Awerintzew, 1906 - 182, 184, 185, 188 (23 5)

*Nebela tubulosa* Penard, 1890 - 196, 197, 198 (17 6)

*Nebela walesi* (Wales) Deflandre, 1936 - 192 (5 9)

*Phryganella acropodia* (Hertwig & Lesser) Hopkinson, 1909 - 183, 185, 192, 193, 195, 197, 199 (41 2)

\* *Phryganella acropodia* var. *depressa* Playfair, 1917 - 196 (5 9)

*Placocista jurasica* Penard, 1905 - 185 (5 9)

*Placocista lens* Penard, 1899 - 190, 200 (11 8)

*Plagiopyxis callida* Penard, 1910 - 185, 188, 189, 190, 191, 192, 193, 195, 196, 197, 198, 199, 200 (76 5)

*Plagiopyxis declivis* Thomas, 1955 - 190, 196 (11 8)

*Plagiopyxis intermedia* Bonnet, 1959 - 198, 200 (11 8)

*Plagiopyxis minuta* Bonnet, 1959 - 197 (5 9)

*Plagiopyxis oblonga* (Bonnet & Thomas) Bonnet & Thomas, 1960 - 184, 191 (11 8)

*Plagiopyxis rostrata* Bonnet, 1974 - 198 (5 9)

*Quadrullella quadrigera* (Wales) Deflandre, 1936 - 190 (5 9)

*Sphenodonta fissirostris* Penard, 1890 - 182, 183, 184, 185, 186, 195, 200 (41 2)

*Tracheleuglypha pulchellum* Bonnet, 1979 - 184, 190, 193 (17 6)

*Tracheleuglypha acolla* Bonnet & Thomas, 1955 - 183, 185, 192, 193, 195, 197 (35 3)

*Tracheleuglypha dentata* (Vejdovsky) Deflandre, 1928 - 185, 186, 188, 191, 192, 193, 197 (41 2)

\* *Tracheleuglypha dentata* var. *elongata* (Playfair) Gauthier-Lièvre & Thomas, 1958 - 188, 193, 195, 196, 200 (29 4)

*Trigonopyxis arcuata* (Leidy) Penard, 1912 - 183, 185, 193, 197, 200 (29 4)

*Trigonopyxis micristoma* Hoogenraad & de Groot, 1948 - 199 (5 9)

*Trinema complanatum* Penard, 1890 - 182, 183, 184, 185, 186, 188, 189, 190, 192, 193, 195, 196, 197, 198, 199, 200 (94 1)

*Trinema complanatum* var. *aenophila* (Declotire) Bonnet & Thomas, 1960 - 182, 183, 185, 191, 193, 195, 196, 197, 199 (52 9)

\* *Trinema complanatum* var. *elongata* Declotire, 1973 - 183, 190, 192, 193, 196, 197 (35 3)

*Trinema complanatum* var. *globulosa* Chardez, 1959 - 184 (5 9)

\* *Trinema complanatum* var. *inflata* Declotire, 1970 - 196, 197 (11 8)

*Trinema complanatum* var. *platystoma* Schonborn, 1964 - 197 (5 9)

*Trinema encheley* (Ehrenberg) Leidy, 1878 - 182, 183, 185, 186, 188, 189, 190, 191, 192, 193, 195, 196, 198, 199, 200 (88 2)

*Trinema encheley* var. *aenophila* Declotire, 1950 - 190, 192 (11 8)

\* *Trinema encheley* var. *naturicola* Declotire, 1962 - 197 (5 9)

*Trinema grandis* (Chardez) Golemansky, 1963 - 188, 192, 193, 195, 196, 197, 200 (41 2)

*Trinema lineare* Penard, 1890 - 183, 184, 185, 186, 188, 189, 191, 192, 193, 195, 196, 197, 198, 199, 200 (88 2)

\* *Trinema lineare* var. *grandis* Declotire, 1971 - 190, 192 (11 8)

*Trinema lineare* var. *truncatum* Chardex, 1964 - 183, 192, 198 (17.6)

\*\* *Trinema staryi* sp. n. - 183, 191, 192, 195 (23.5)

\* *Valkanovia delicatula* (Valkanov) Tappan, 1966 - 196 (5.9)

#### Faunistical and ecological characteristics of testate amoebae assemblages

On the basis of a soil and leaf litter samples analysis from the primary rain forest in the northern part of Vietnam 126 species, varieties and forms of testate amoebae were determined. These testate amoebae belong to 10 families and 23 genera. The most abundant families were Euglyphidae (34 species), Centropyxidae (29 species), Hyalospheniidae (24 species) and Trinematidae (17 species). From the genera *Euglypha* (21 species), *Centropyxis* (20 species), *Trinema* (14 species) and *Nebela* (10 species) were most abundant. In the Fig. 2 the distribution of the most abundant 7 testate amoebae families in single samples is represented.

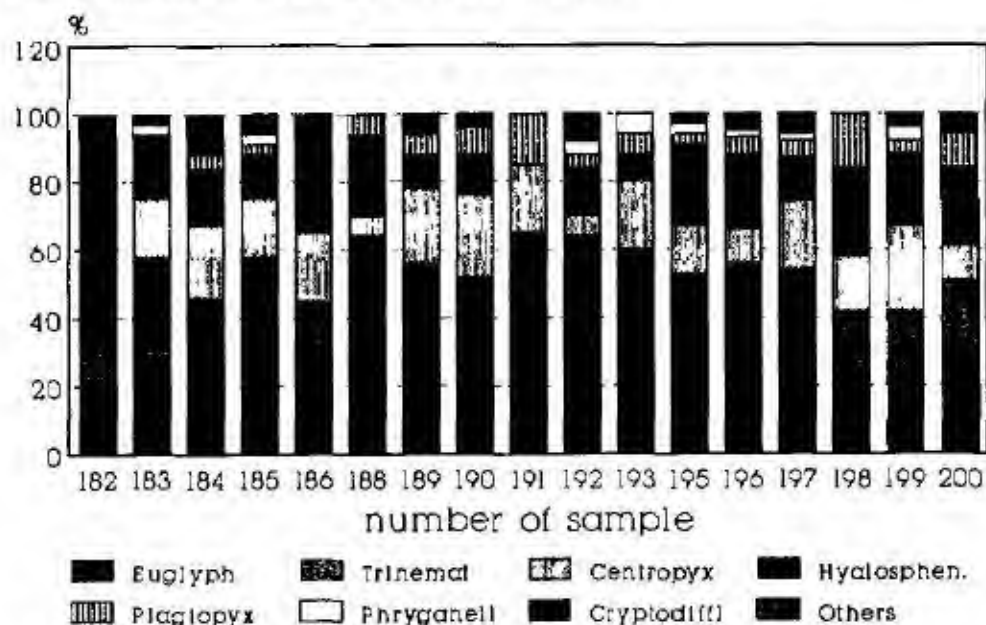


Fig. 2. Distribution of the testate amoebae families in the samples.

Comparing the determined data with the literature about the south-eastern Asia testaceans it is evident that the testate amoebae fauna of Vietnam has similar parameters. It is rich in species composition, but less genera and families are represented here (for example: Bonnet, 1981 - Thailand - 104 species, 31 genera; Bonnet, 1980 - Philippines - 110 species, 38 genera; Bonnet, 1980 - Papua-New Guinea - 121 species, 35 genera; Bonnet, 1977 - Nepal - 130 species, 37 genera; Bartoš, 1963 - Java - 77 species, 21 genera).

In the studied communities families which are common in the forest soils in temperate zone are absent (*Microchlamyidae*, *Paraquadrulidae*, *Lesquereusiidae*, *Amphitrematidae*, *Gromiidae*

and Cyphoderidae) or in the soils of tropical zone (Distomatopyxidae, Lamtopyxidae). In the represented families are absent many genera (for example *Geopyxella*, *Schwabia*, *Pseudawerintzewia*, *Bulinularia*, *Pontigulasia*, *Cryptodiffugia*).

Frequency over 50 % was reached in the species *Centropyxis deflandriana*, *Corythion dubium*, *Euglypha cristata*, *E. laevis*, *E. rotunda*, *E. tuberculata*, *Heleopera minuta*, *Plagiopyxis callida*, *Trinema complanatum*, *T. complanatum* var. *aerophila*, *T. enchelys* and *T. lineare*.

The composition of the studied communities was in principle similar to the composition of the testate amoebae communities in the cited papers (the majority of the members in the families Centropyxidae, Euglyphidae, Hyalospheniidae and Trinematidae). Differences were found in rare species.

In the studied testate amoebae communities several very well determined groups of species were represented. The first group is composed of cosmopolitan species (often euryvalent species), which are common in all ecosystems on the Earth (for example *Centropyxis aerophila*, *Corythion dubium*, *Assulina muscorum*, *Euglypha laevis*, *E. rotunda*, *Phryganella acropodia*, *Trinema complanatum*, *T. enchelys*, *T. lineare*). The second group are "tropical" species, which were known up to this time from the tropical zone only (for example *Centropyxis latideflandriana*, *C. protecta*, *C. stenodeflandriana*, *Cyclopyxis quadratus* var. *grandis* var. n., *C. stephanostoma*, *C. trilobata*, *Deharvengia papuensis*, *Heleopera alsiosa*, *Hyalosphenia tamdaoensis* sp. n., *H. schoutedeni*, *H. schoutedeni* var. *rotundata*, *Plagiopyxis rostrata*, *Quadrullella quadrigera*, *Trinema enchelys* var. *aerophila*, *T. enchelys* var. *nasurticola* and *T. staryi* sp. n.). The rest are specialized species (moss-inhabiting, sphagnum-inhabiting), which were determined up to this time in some continents and probably these species are cosmopolitan.

From ecological groups especially the species of the moist and very moist substrates (no aquatic species) were represented here - for example *Assulina muscorum*, *Centropyxis aculeata*, *Cyclopyxis humilis*, *Diffugia lucida*, *Euglypha cristata* and its varieties, *E. filifera*, *Hyalosphenia papilio*, *Trigonopyxis arcuata*. The euryvalent species were represented with *Centropyxis aerophila*, *Cyclopyxis kahli*, *Euglypha laevis*, *E. rotunda*, *Corythion dubium*, *Nebela militaris*, *Heleopera petricola*, *Phryganella acropodia*, *Tracheleuglypha acolla* and *Trinema lineare*. The soil species were found in the low numbers (for example *Centropyxis cornuta*, *C. ovalis*, *Cyclopyxis eurystoma* var. *grandis*, *Heleopera alsiosa*, *Trinema lineare* var. *grandis*).

The samples of soil and litter were removed so that the variability of biotope was recorded (undisintegrated leaf litter, disintegrated leaf litter, arthropodic moder, very moist humic soil, moist soil without plant cover and plant rests). The communities in the studied biotope were relatively unsimilar and heterogenous. For evaluating community homogeneity (or heterogeneity) the Sørensen index of faunistic similarity at the species and genera levels (Fig. 3 and Fig. 4) was applied. On the species level (Fig. 3) the lowest similarity among the sample 182 and all other samples (8.3 - 27.6 %) was determined. The highest similarity was found between the samples 188 and 200 (58.3 %). Altogether the faunistic similarity on the species level was relatively low. On the genera level of Sørensen index of faunistic similarity (Fig. 4) the lowest value was found among the sample 182 and other samples (15.4 - 62.5 %). The highest values of faunistic similarity were determined among the samples 188 and 198 (94.1 %), 185 and 200 (93.3 %), 183 and 185 (88.9 %), 195 and 196 (88.0 %). The faunistic similarity on the genera level was more expressive than that on the species level. Those data give evidence that the testate amoebae communities in the soil and litter of primary rain forest are very dependent on microhabitats. Single microhabitats are different in physical and pedological characteristics and these differences determine the composition of the testate amoebae community on the individual habitat. In the Table 1 number values of species and genera are presented. These data verify the heterogeneity of the testate amoebae communities in the soil and litter of the primary rain forest near Tam-Dao.

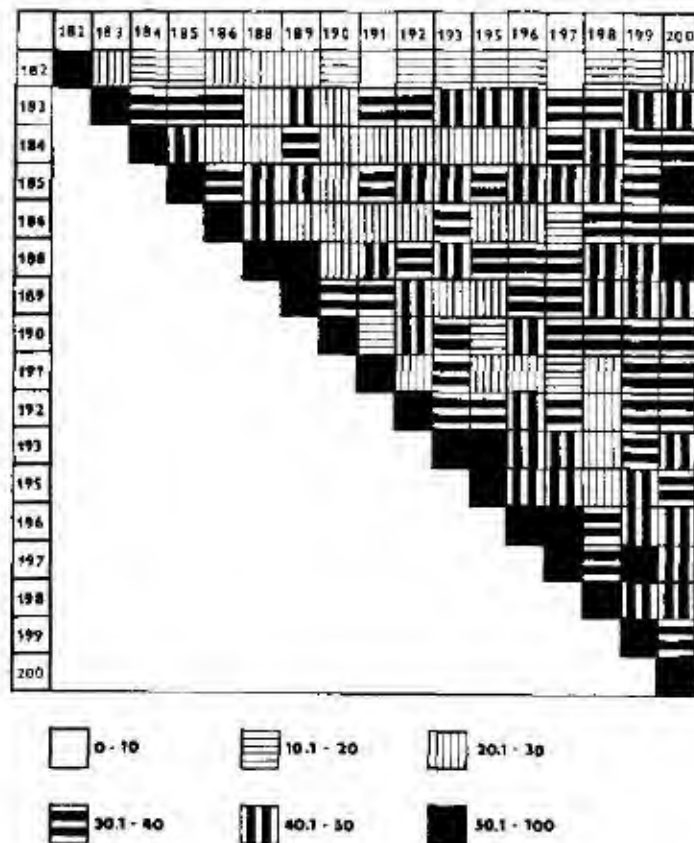


Fig. 3. Sørensen's index values at the species level.

Abundances, numbers of species and genera in particular samples were very different (Table 1). The lowest abundance was found in the sample 182 (58 500 ex.g<sup>-1</sup>), the highest one in the sample 196 (144 900 ex.g<sup>-1</sup>). The lowest number of species was determined in the sample 182 (10 species), the highest one in the sample 196 (41 species). The lowest number of genera was found in the samples 182 and 191 (6 genera), the highest one in the samples 185 and 200 (15 genera).

The LF index after Bonnet (1964) (Table 1) - Testaceafilosa/Testacealobosa ratio - was, except the sample 186, negative (LF: from -0.4 to -0.03). This fact gives evidence that in the individual testate amoebae communities the members of the Testaceafilosa were predominant. The majority of members of Testaceafilosa group is (after Bonnet) the mark of the unstabilized (quickly developing) soil testate amoebae community.

The dimensions of the shells of all determined species were measured in the upper limit of the in the literature cited dimensions. Little shells were rare in species populations. In testate amoebae communities many varieties of typical species which differ in their sizes were determined (for example *Cyclopyxis eurystoma* var. *grandis*, *C. quadratus* var. *grandis*, *Tracheleuglyphia dentata* var. *elongata*, *Trinema complanatum* var. *elongata*, *T. lineare* var. *grandis*). The new



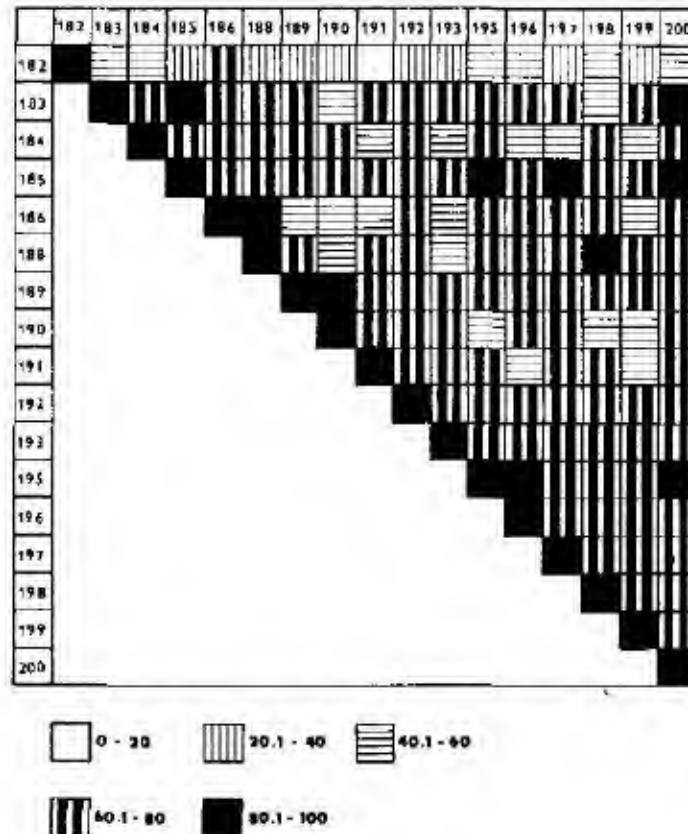


Fig. 4 Sørensen's index values at the genera level.

species *Trinema staryi* is up to this time the greatest species of this genera. The majority of large forms of testaceans is a symptom of good ecological and life conditions in the studied area (high moisture, temperature, sufficient number of food etc.).

#### Descriptions of new species for science

##### *Cyclopyxis quadratus* var. *grandis* var. n. (Fig. 5)

**DESCRIPTION.** Shell by ventral view tetragonal (square, oblong or trapezium) with rounded edges. By side view shell vaulted, almost hemispherical. The organic matter of shell covered with large, flat, polygonal mineral particles. The shell translucent, light brown-gray or light rusty brown. The aperture round or breath oval with undulated rim, uninvginated, in the centre of the bottom side of the shell. From the nominate form *Cyclopyxis quadratus* Decloître differ with its large dimensions only.

**PROTOPLASM.** Not observed, only empty shells or encysted individuals were observed. In encysted individuals there is only one dark brown globular cyst, with smooth surface in the shell.

Table 1. Number of species (NS), number of genera (NG), abundance in ind. g<sup>-1</sup> (A) and values of LF-index (LF) in single samples

Sample No	NS	NG	A	LF
182	10	6	58 500	-0.40
183	31	10	88 800	-0.16
184	24	10	81 000	-0.08
185	31	15	96 000	-0.16
186	20	9	76 200	0.00
188	17	9	65 700	-0.29
189	18	10	73 800	-0.11
190	21	12	94 500	-0.14
191	15	6	59 700	-0.33
192	28	11	74 400	-0.36
193	25	11	95 400	-0.20
195	29	12	108 600	-0.03
196	41	12	144 900	-0.17
197	39	14	124 500	-0.03
198	20	9	72 900	-0.10
199	24	10	68 400	-0.25
200	31	15	89 700	-0.03

DIMENSIONS. Length 148 - 158 µm, breadth 146 - 157 µm, height 70 - 76 µm, diameter of aperture 62 - 69 µm (biometrical characteristics see Table 2).

HOLOTYPE DIMENSIONS. Length 150 µm, breadth 149 µm, height 72 µm, diameter of aperture 63 µm (Fig. 5a and 5c)

LOCUS TYPICUS. Vietnam, Tam-Dao, primary mountain rain forest, sample No. 189, very disintegrated leaf litter. Leg. J. Starý. 12 individuals (7 empty shells, 5 encysted individuals)

ECOLOGY. *Cyclopyxis quadratus* (nominate form) was found in the leaf litter of the vine and "arbre de Judée" in the neighbourhood of the Var city in France. A new variety was determined in very disintegrated leaf litter from a tropical rain forest. It is clear, that the nominate form and new variety are fixed on the disintegrated leaf litter.

TYPE MATERIAL. Holotype and 2 paratype slides are deposited in the author's collection of permanent slides, Institute of Soil Biology, Academy of Sciences of the Czech Republic, České Budějovice

DERIVATIO NOMINIS. New variety is called according the size difference from the nominate form *Cyclopyxis quadratus*.

Table 2. Biometrical characteristics of *Cyclopyxis quadratus* var. *grandis* var. n. (x - arithmetical mean, M - median, s - standard deviation, V - coefficient of variation in %, Min - minimum, Max - maximum, n - number of investigated individuals, all dimensions in µm)

	x	M	s	V	Min	Max	n
length	153.75	155.00	3.36	2.19	148.0	159.0	12
breadth	151.66	152.00	3.45	2.27	146.0	157.0	12
height	72.75	72.50	2.26	3.11	70.0	76.0	12
diameter of aperture	66.00	66.00	2.25	3.42	62.0	69.0	12



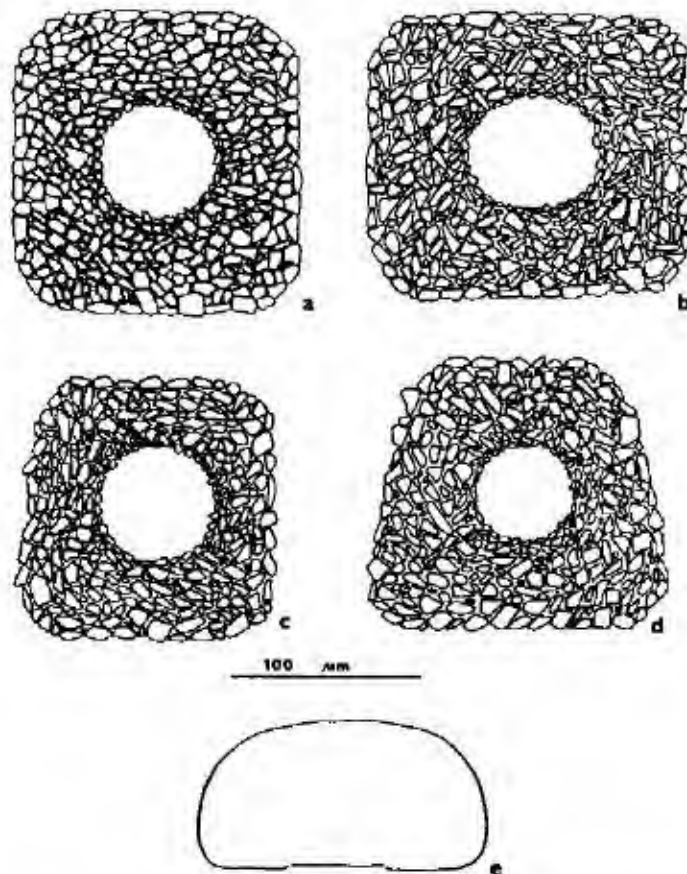


Fig 5 *Cyclopyxis quadratus* var *grandis* var *n.* (a, b, c, d - ventral view, e - lateral view).

*Hyalosphenia tamdaoensis* sp. n. (Fig. 6)

**DESCRIPTION.** Shell bilaterally symmetrical, long, narrow oval, egg-shaped or vase-shaped, on the cross section bean-shaped or kidney-shaped. Dorsal side vaulted, ventral side depressed, depression elliptical. Shell from the organic matter only, with relative robust shell wall, surface smooth. Lateral pores absent. Shell pellucid, translucent, light yellow or yellow-orange. Aperture small, elliptical, with thick rim.

**PROTOPLASM.** Not observed, only empty shells were observed.

**DIMENSIONS.** Length 107 - 115 μm, breadth 31 - 36 μm, thickness 9 - 15 μm, thickness of the shell wall 1 - 2.5 μm, aperture 9 - 11 x 3 - 6 μm, elliptical depression 76 - 88 x 17 - 23 μm (biometrical characteristics see Table 3).

**HOLOTYPE DIMENSIONS.** Length 110 μm, breadth 32 μm, thickness 10 μm, thickness of the shell wall 1.5 μm, aperture 10 x 4 μm, elliptical depression 79 x 20 μm (Fig. 6 a - d).

Table 3. Biometrical characteristics of *Hyalosphenia tamdaoensis* sp. n. (explanatory notes see Table 2)

	x	M	s	V	Min	Max	n
length	110.75	110.50	2.33	2.10	107.0	115.0	8
breadth	33.34	33.00	1.59	4.79	31.0	36.0	8
thickness	12.00	12.00	1.93	16.06	9.0	15.0	8
breadth of aperture	9.63	9.00	0.92	9.51	9.0	11.0	8
length of aperture	3.88	3.50	1.13	29.02	3.0	6.0	8

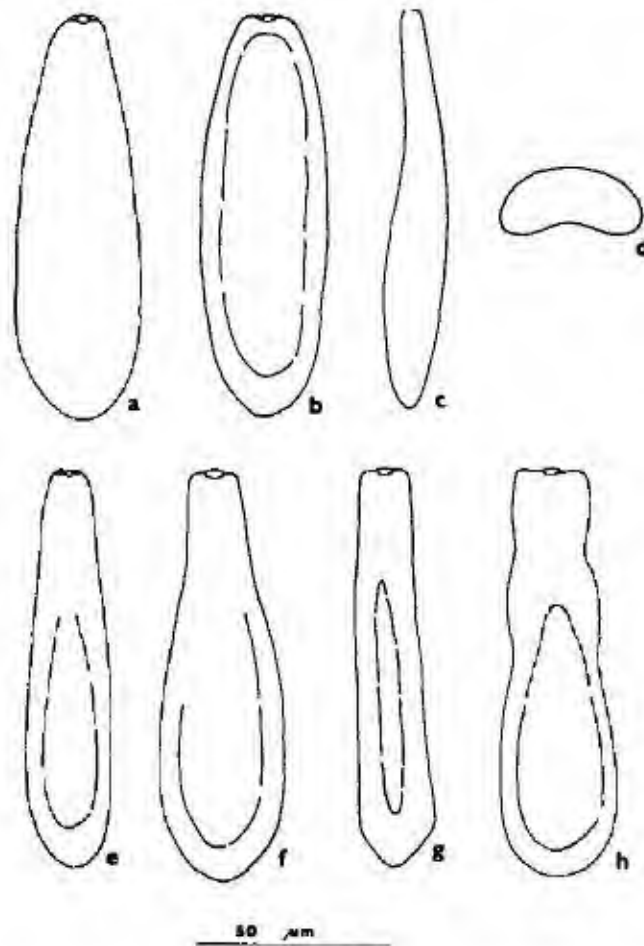


Fig. 6. *Hyalosphenia tamdaoensis* sp. n. (a - dorsal view; b, e, f, g, h - ventral view; c - lateral view; d - cross section).

LOCUS TYPICUS. Vietnam, Tam-Dao, primary mountain rain forest, sample No. 196, arthropodic moder mixed with the very disintegrated leaf litter, leg. J. Stary, 8 empty shells.

ECOLOGY. The shell shape signalizes, that this species is the soil inhabitant with the typical ecological adaptation (thin, arched shell, small aperture). This species is probably attached to humic soil horizon.

TAXONOMICAL COMMENTS. Shells of this species are similar to those of the *Hyalosphenia subflava*, *H. schoutedeni* and *H. gigantea* de Graaf. The new species differs in its dimensions the following ones (greater than *H. subflava* and *H. schoutedeni*, smaller than *H. gigantea*), further on a different pseudostom shape (aperture is smaller in its dimensions than the apertures of all three above-mentioned species), loss of lateral pores and general shape (depression of the shell).

TYPE MATERIAL. Holotype and two paratype slides are deposited in the author's collection of the permanent slides, Institute of Soil Biology, Academy of Sciences of the Czech Republic, České Budějovice.

DERIVATIO NOMINIS. The species name "*tamdaoensis*" was elected after the studied locality (Tam-Dao).

#### *Trinema staryi* sp. n. (Fig. 7)

DESCRIPTION. Great shell in the ventral and lateral view drop-shaped, dorsoventrally strong depressed. Shell from hyaline, colourless organic matter. On the surface of the shell there are great isolated round plates, the spaces among them are filled with small round plates. The shell translucent, pellucid, colorless. The aperture rounded, great, in the narrow and low part of the shell. The periphery of the aperture are bordered with small dents.

PROTOPLASM. Translucent, pellucid, colorless. One nucleus, 1 - 5 vacuoles. Pseudopodia filopodia-type, thin, thread-like, in different lengths, non-anastomose. Epipodia thin, thread-like.

DIMENSIONS. Length 196 - 248  $\mu$ m, breadth 148 - 212  $\mu$ m, thickness 48 - 64  $\mu$ m, diameter of aperture 64 - 79  $\mu$ m, diameter of great plates 16 - 20  $\mu$ m, diameter of small plates 2 - 4  $\mu$ m (biometrical characteristics see Table 4).

HOLOTYPE DIMENSIONS. Length 240  $\mu$ m, breadth 206  $\mu$ m, thickness 55  $\mu$ m, diameter of aperture, 69  $\mu$ m, diameter of great plates 17  $\mu$ m, diameter of small plates, 2  $\mu$ m (Fig. 7 a - b).

LOCUS TYPICUS. Vietnam, Tam-Dao, primary mountain rain forest, samples 183, 191, 192 and 195, humic soil horizon, mixture of the disintegrated leaf litter and mineral particles. Leg. J. Stary. 30 shells were measured. In samples were found many empty shells and live individuals.

ECOLOGY. This species is probably connected with the moist humic soil horizon. The flattened shell signalize the tolerance to the moisture fluctuations. The food of this species was composed of bacteria and organic detritus (after the food vacuoles content).

Table 4. Biometrical characteristics of *Trinema staryi* sp. n. (explanatory notes see Table 2)

	$\bar{x}$	M	s	V	Min	Max	n
length	224.63	228.50	16.05	7.15	196.0	248.0	30
breadth	175.93	176.50	20.94	11.90	148.0	212.0	30
thickness	56.03	55.50	4.83	8.62	48.0	64.0	30
diameter of aperture	71.10	73.00	4.46	6.27	64.0	79.0	30

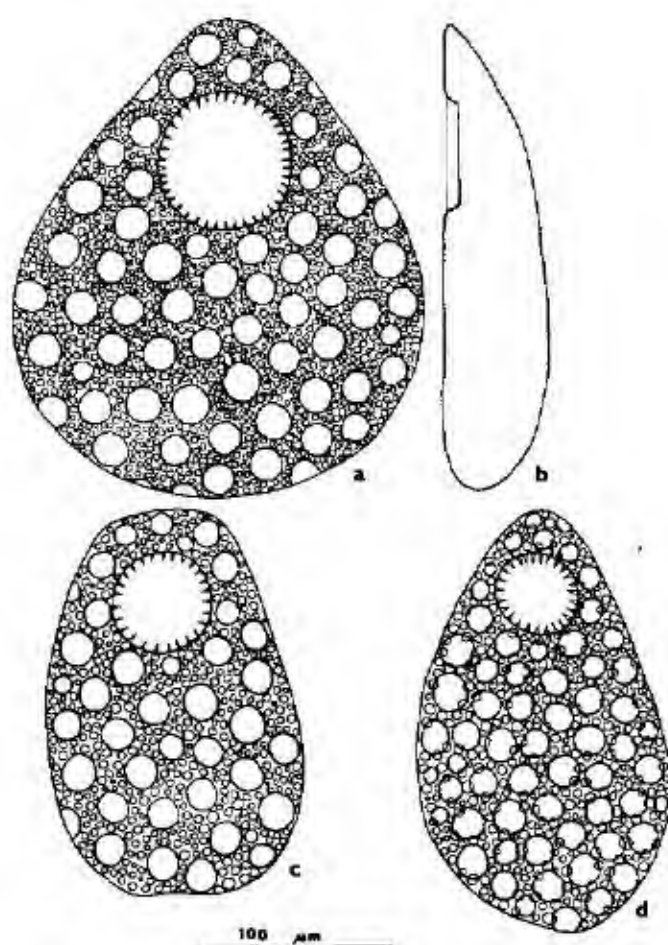


Fig. 7 *Trinema staryi* sp. n. (a, c, d - ventral view, b - lateral view)

**TAXONOMICAL COMMENTS.** This species is similar (in the shape) to *Trinema grandis* and differ from it by the dimensions (the greatest member of the genus *Trinema*) and by the plates arrangement on the shell surface.

**TYPE MATERIAL.** Holotype and 4 paratype slides are deposited in the author's permanent slide collection, Institute of Soil Biology, Academy of Sciences of the Czech Republic, České Budějovice

**DERIVATIO NOMINIS.** This species is dedicated to the soil oribatid mites specialist Dr Josef Stary from the Institute of Soil Biology, České Budějovice

## Acknowledgements

I thank to Dr Josef Stary (Institute of Soil Biology, AS CR, České Budějovice) for the providing soil and litter samples to the study of testate amoebae fauna of Vietnam, to Dr Josef Rusek (Institute of Soil Biology, AS CR, České Budějovice) for the criticism to this manuscript and to Mr Josef Kult for the linguistic corrections

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## Geographic variation in three species of *Myotis* (Mammalia: Chiroptera) in South of the Western Palearctics

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Received December 20, 1994; accepted February 9, 1995

Published June 22, 1995

**Biometrics, bats, geographic variation, clines, Mediterranean, biogeography**

**Abstract.** A morphometrical study of a large sample (1348 specimens) of three *Myotis* spp. (*M. myotis*, *M. blythi*, *M. nattereri* s.l.) revealed in all three taxa a clinal variation in cranial measurements from the Western Mediterranean via Central Europe and Balkans to the Eastern Mediterranean. The trend of size increase from West to East terminated in the Ponto-Caspian region. Nevertheless, being the marginal populations excluded, the geographically dependent morphometric variation is insignificant. Hence, the populations of Central Europe, Balkans and Eastern Mediterranean are relatively homogenous as to their variation pattern and, in contrast to those of Ponto-Caspian region and/or of the Western Mediterranean show no isolation-by-distance variation.

### INTRODUCTION

The pattern of geographic variation ranks among the most important characteristics of any taxon. It may provide a complex information on internal structure of the taxon, its adaptation dynamics and/or on history of its distribution. Anyhow, such a type information is accessible only through a detailed analysis of quite a large material of population samples covering both the distribution range of the taxon and the traits responsible for its phenotypic variation as completely as possible (Gould & Johnston 1972, Thorpe 1985, 1987).

In bats, such studies are often limited due to actual rarity of most species and scarcity of materials, particularly those of the marginal populations. Thus, it is not surprising that only very few studies are available that deal with geographic variation of chiropteran species in details, and analyze also the possible factors responsible for the observed patterns of variation (Findley & Wilson 1982, Findley 1992). As concerns vespertilionids that became subject of such studies much more frequently than any other bats, such investigations have been undertaken e.g. with *Pipistrellus hesperus* (Findley & Traut 1970), *Myotis lucifugus* and *M. fortidens* (Findley & Jones 1967), *Myotis californicus* (Bogan 1975), *Eptesicus fuscus* (Burnett 1983), *Myotis blythi* (Strelkov 1972) or with *Myotis daubentonii* (Bogdanowicz 1990).

Studying morphometric variation in two W-Palearctic sibling species, *Myotis myotis* and *M. blythi*, we found (similarly to the above mentioned studies) a clear cline variation in size (Benda & Horáček 1995), parallel in both the species. Appearance of such a parallelism can generally be regarded a phenomenon of a considerable interest. It may either reflect mutual ecological relations between the species (e.g. in form of a character displacement) or appearance of a geographical gradient in some environmental currents affecting the respective populations. The previous paper (Benda & Horáček 1995) discussed the former possibility, this one is focused to the latter aspect. To assess a validity of the latter alternative, one should enlarge a set of the species under comparison with some other sympatric forms not coming in actual ecological interactions. In respect to



the material available, we take in comparison *Myotis nattereri*. Although it is a gleaner, similarly like the two species under discussion, in its diet, in hunting grounds and/or in roost preferences it differs from the two mentioned species quite a much (cf. Bauerová 1978, Bauerová & Červený 1986, Arlettaz 1994, Červený & Horáček 1981). Moreover, *Myotis nattereri* and related species became already a subject of a detailed morphometrical study (Horáček & Hanák 1984) though it has not been focused to the topics under discussion.

Similarly as in the case of the other two species, the metrical data on which the above mentioned papers were based has not been published as yet.

Consequently, this paper is intended to (1) provide a survey of the primary biometrical data for whole the material discussed in the above mentioned previous papers (i.e., Horáček & Hanák 1984, Benda 1994, Benda & Horáček 1995), (2) evaluate major patterns of the geographical variation in the Western Palearctic range in each of the species under study, and (3) compare all three species from this viewpoint and discuss possible biogeographic phenomena revealed from the differences and/or similarities among them.

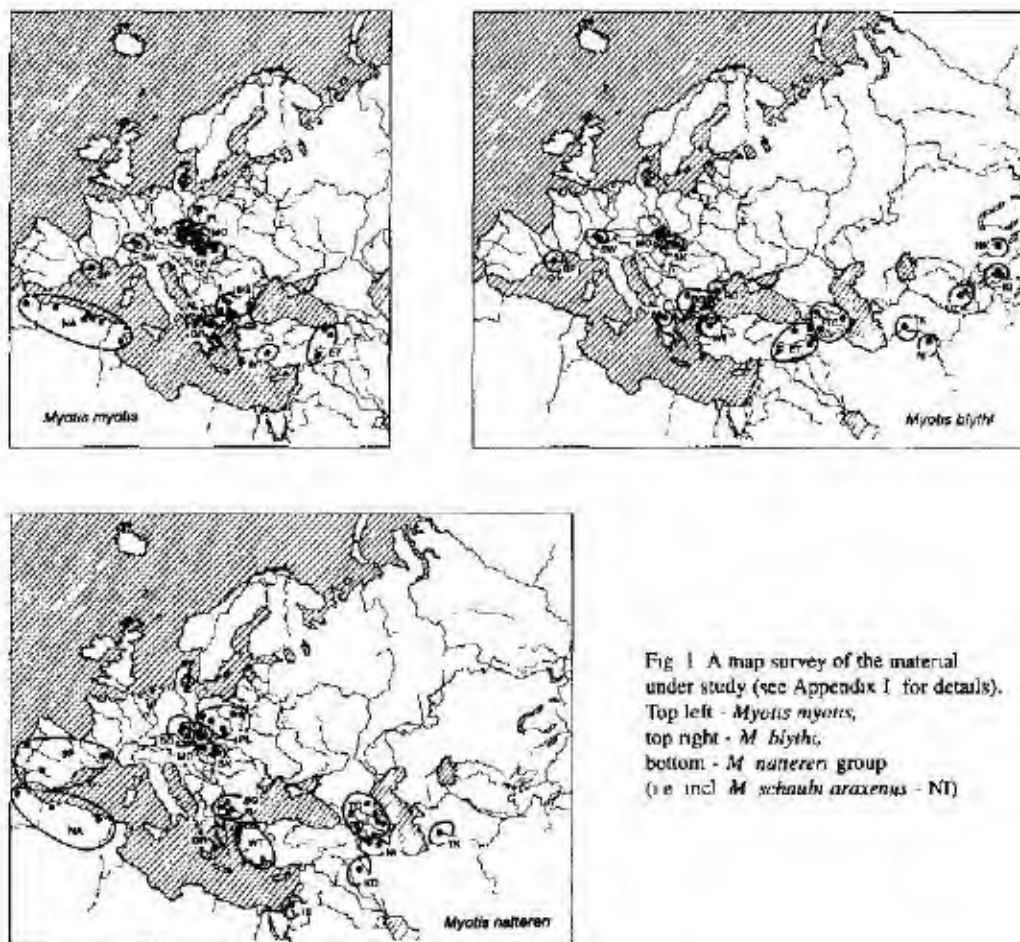


Fig. 1. A map survey of the material under study (see Appendix I for details).  
Top left - *Myotis myotis*,  
top right - *M. blythi*,  
bottom - *M. nattereri* group  
(i.e. incl. *M. schaubi araxensis* - NI)



## MATERIAL AND METHODS

The paper is based on an extensive sample of museum specimens, in total amounting to 1348 adult individuals, viz. 717 ind. of *Myotis myotis* (Borkhausen, 1797), 425 *Myotis blythi* (Tomes, 1857), and 206 in *Myotis nattereri* group - including *Myotis nattereri* (Kuhl, 1818), *M. schaubi araxenus* (Dahl, 1947), and other named local forms in sense of Horáček & Hanák (1984). For more details on source of the material see Appendix 1 and Fig. 1a-c.

The comparisons are based on 28 cranial characters including 26 measurements, external measurements has not been evaluated in this paper. All the respective characters are surveyed in Appendix 2. The standard cranial dimensions were measured with aid of a calliper, dental measurements were taken by a stereomicroscope equipped with measuring device.

In each species, the total sample was subdivided into subsets based on the source areas, which then were treated separately. We computed basic statistics for each subset and compared the subsets with aid of both the primary data and the statistical characteristics using more uni-, bi- and multivariate techniques.

The geographic regions were delimited more or less arbitrarily in respect to actual amount of the material available from a region as well as a distance of a sample from neighbouring source areas. In contrast to central Europe where a large amount of material was available for each species and each geographically delimited subset, some marginal areas were represented with quite poor samples only.

For simplicity sake, in this paper, we refer (because of the reasons mentioned elsewhere - Benda & Horáček 1995) the samples of the North African form, *Myotis* (*M. blythi* or *M. myotis*) *punicus*, to *Myotis myotis*, without neglecting all uncertainties concerning its actual status. Correspondingly, due to reasons summarized by Horáček & Hanák (1984) "*Myotis nattereri araxenus*" is here considered as an independent species, *M. schaubi araxenus*.

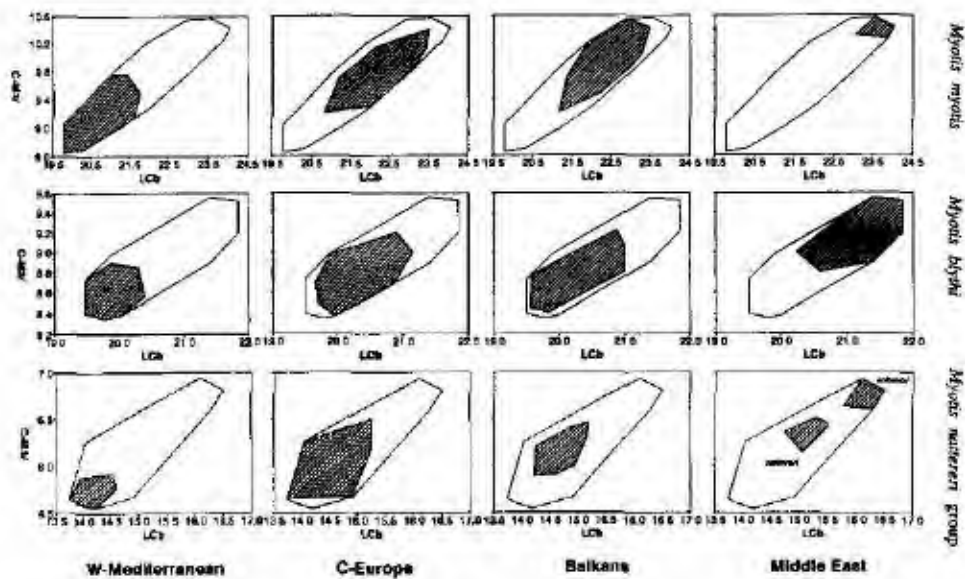


Fig. 2. A bivariate plot of condylobasal length (LCb) vs. length of upper tooth row (CM3) in three species under study. Line polygons refer to marginal values in total samples of individual species, dashed clouds to those in the sets respective to the Western Mediterranean (NA, SP), Central Europe (SW, BO, MO, PL, SK), Balkans (AL, RO, BG, GR, WT) and the Middle East (ET, KD, TC, NI).

## RESULTS

In general, an average amount of variation in total samples were almost the same for each species (coefficients of variation for individuals characters varied from 0.023 to 0.090, being generally the highest in the premolar row including dental lengths, viz. C-P4, P1-P4). In this respect, only minute differences were found among the species as well as among the individual samples.

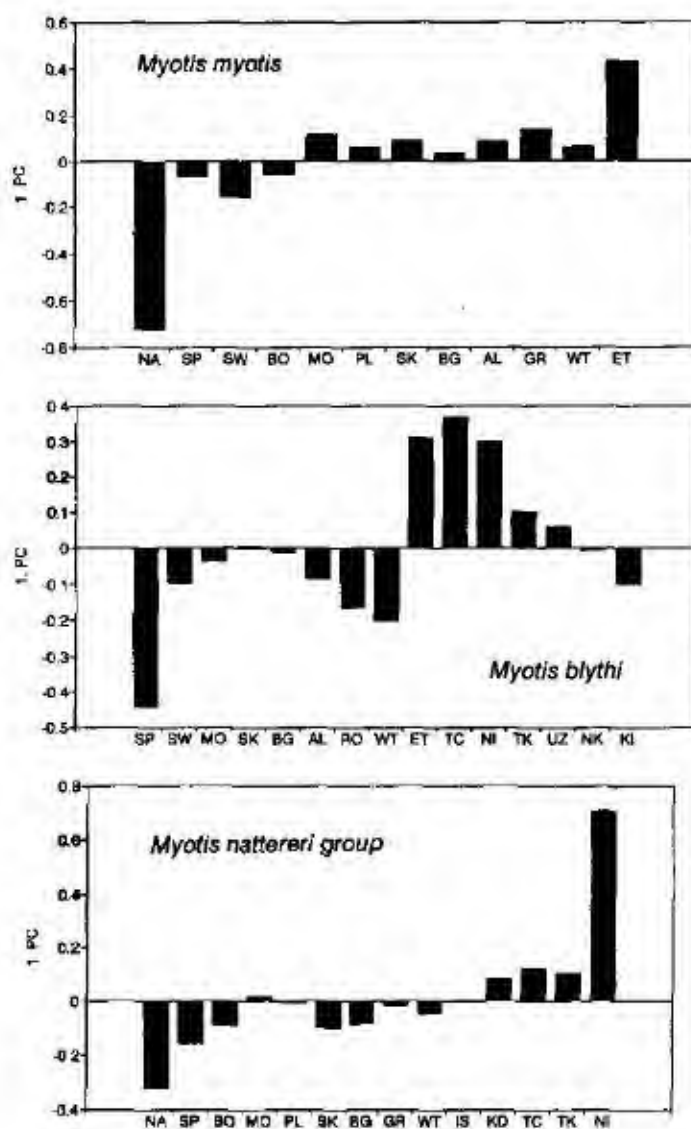


Fig. 3. Values of the 1st principal component (expressing a size aspect) in individual samples of each respective species (computed for each species separately), arranged along West-East direction.





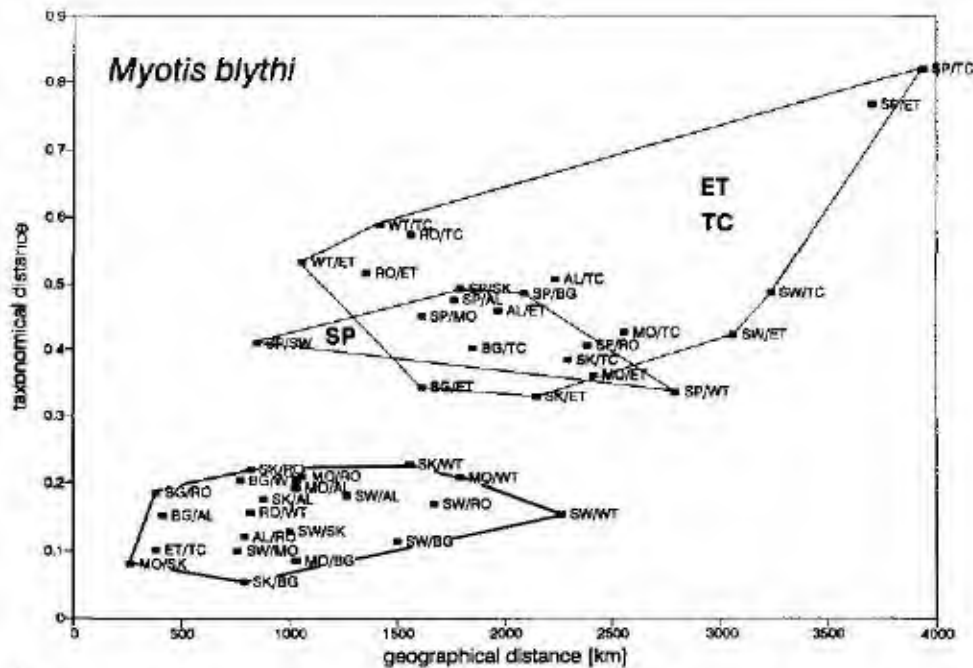


Fig. 6. Generalized taxonomical distances between each pair of samples plotted against the geographical distances of the respective populations. *M. blythi*: distances from marginal populations, SP and ET-TC, and those among remaining samples (those of Central Asia being excluded) separated by line polygons.

being the above mentioned marginal populations removed, the respective correlations become very faint only, and invariably, insignificant (Tab. 1, Fig. 5-8). Consequently, it indicates, that in respect to geographic size variation, the populations of Central Europe, Balkans and the Eastern Mediterranean s.str. are homogenous and in this character showing no significant isolation-by-distance pattern. Although the above mentioned marginal populations represent only a minute part of total sample, as a rule, excluding them, a mean character variation of the total samples decreases considerably (12.1% in *M. nattereri*, 15% in *M. myotis*, 4.7% in *M. blythi*).

The greatly pronounced mutual differences among the marginal populations and remaining ones (as mentioned above) indicate the general pattern of geographic variation in all three taxa is of a categorial (Thorpe 1987) or "stepped cline" (Grant 1972) type rather than a smooth cline variation as expected on the basis of the univariate or bivariate comparisons.

#### DISCUSSION AND CONCLUSIONS

An overall clinal increase in size, parallel in all three taxa under study, represents apparently the first point that is to be discussed. In the western Palearctic, a body size increase from West to East is known to occur in more mammalian species. In great majority this concerns, of course, the elements of the boreal zone - shrews such as *Sorex caecutiens*, *S. isodon* (Dolgov 1972) or more rodents (Gromov & Poljakov 1977, Dupal 1987) which E-European and W-Siberian forms are generally considerably larger than those of the W- and Central Europe. This also concerns bats,





e.g. *Myotis daubentonii* (Hanák & Horáček 1984, Bogdanowicz 1990) or *Vespertilio murinus*. In all these cases, similarly as in most of other instances when clinal variation in body size was observed (Findley & Jones 1967, Findley & Traut 1972, Burnett 1983), a good correspondence with increasing climatic severity suggests which kind factors may be responsible for the phenomenon. Body size is here looked upon as inversely related to temperature, correspondingly to the South - North cline, which general appearance in many taxa became the primary source of the classical form of Bergmann's (1847) rule (for details and a number of examples see e.g. Panteleev 1983).

Appearance of a size increase cline from West to East in the Mediterranean region can hardly be explained in that way, of course. At the same time, it is to be stressed that this cline appears parallel not only in three species under study but supposedly in more other forms of the ponto-mediterranean distribution - *Rhinolophus ferrumequinum* can serve here as a good example (de Paz 1994). James (1970) discussing geographic variation in the North American birds demonstrated that body size often exhibits a better negative correlation with environmental moisture than with temperature. In these connections he proposed a corrected form of Bergmann's rule: "Intraspecific variation in homeotherms is related to a combination of climatic variables that includes temperature and moisture. Small size is associated with hot humid conditions, larger size with cooler or drier conditions". The previous studies on chiropteran geographic variation indicated, in contrast to temperature, rather a positive relation between body size and moisture (Burnett 1983, Bogdanowicz 1990), which contradicts James's (1970) concept. Such a situation has been explained by metabolic specificities of bats that enable them to balance stressing effect of low environmental moisture without necessitating to reduce surface area to volume ratio (cf. Burnett 1983).

The situation revealed in the Mediterranean region, where temperature is generally relatively high, while precipitation dramatically decreases from West to East (Riper 1971) could, in contrast, indicate a validity of the moisture factor.

Nevertheless, as indicated by our results, such a view is justified only on a very rough scale, i.e. when evaluating an overall pattern within an area from the western-most Mediterranean to North-western Iran. In each three taxa, the West Palearctic populations can be easily subdivided into three different groups - those of the smallest body size in the Western Mediterranean, the medium sized in Central Europe and Eastern Mediterranean and the large-sized in the Ponto-Caspian region. Our data indicates that transitions among them are most probably not gradual. The situation within the region occupied by medium-sized forms suggests only faint if any geographically dependent size variation - in any case, much lesser than could be predicted based on the overall cline pattern. This not only substantiates the taxonomical conclusions proposed in our previous papers (Horáček & Hanák 1984, Benda & Horáček 1995) that all three allopatric groups are to be taxonomically separated (on a subspecific level in case of *M. myotis* and *M. blythi*, on a species level in case of *M. schaubi araxenus*) but also indicates that all three respective regions do indeed represent quite a different biogeographical units (cf. de Lattin 1967 for

Figs 7 - 8. Generalized taxonomical distances between each pair of samples plotted against the geographical distances of the respective populations: 7 - *M. nattereri* group: distances from marginal populations, NI (*M. schaubi araxenus*) and NA-KD, and those among remaining samples (except for TK) separated by line polygons; 8 - *M. nattereri* s. str. distances from marginal populations, NA, TK, KD, SP, and those among remaining samples separated by line polygons

a comparison) possessing specific patterns of selection conditions, different from those in other regions.

Among other it also claims for that the data on geographic variation in morphometrical characters were complemented with results of a through study of the chorological and ecological specificities of these regions, their mutual relations in all these respects, and with a study of significance of these factors for the West Palearctic faunal evolution.

#### Acknowledgements

The authors wish to thank to all the colleagues who enabled them to study the materials under their care and/or kindly discuss the topics. Namely these were: M. Anděra (Prague), R. Arlettaz (Lausanne), K. Bauer (Vienna), B. Beneš (Opava), J. Garsler (Brno), H. Hackethal (Berlin), V. Hanák (Prague), J. E. Hill (London), L. Hérku (Píseň), W. Issel (Augsburg), D. Kock (Frankfurt a. M.), K. Kowalski (Krakow), B. Kryštufek (Ljubljana), H. Mendelsohn (Tel Aviv), I. Ja. Pavlinov (Moscow), I. K. Rachmatulina (Baku), O. L. Rossolimo (Moscow), A. L. Ruprecht (Białowieża), N. S. Rybin (Oš), F. Spitzenberger (Vienna), H. M. Steiner (Vienna), P. P. Strelkov (St. Petersburg), G. Storch (Frankfurt a. M.), G. Topál (Budapest), V. Vohralík (Prague), B. W. Woloszyn (Krakow), J. Zima (Brno). Special thanks go to Prof. Dr V. Hanák for critical reading of the manuscript and valuable comments. The study was supported by a grant GA CR 204/93/0531 (JH).

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#### APPENDIX I – SURVEY OF MATERIAL UNDER STUDY

For each geographic sample, the following data are provided: (a) locality (district), (b) collection (for abbreviations see Appendix II), (c) number of specimens (m = males, f = females, x = sex undetermined)

##### *Myotis myotis*

**NA-NORTH AFRICA:** Morocco: Taza (Taza) UL 2m, Algeria: Aokas cave (Bejaia) MUB 27m, 18f, Ouhran (Ouhran) MUB 2f, Sook el Tnine (Bejaia) M-UB 3f, Tiddis (Constantine) MUB 4m; Tiddja (Lalla Kadidja) MUB 2m; Yakouren (Azazga) MUB 1m, Tunisia: El Djem ISZ 10m, 2f, Tunis (Tunis) MG 1m

**SP-SPAIN:** Barcelona (Cataluña) UL 2m

**SW-SWITZERLAND:** Corsier (Vaud) UL 5x; Chippis (Valais) UL 1x; Pully (Valais) UL 3f, 2x; Rurogne (Valais) UL 1m, 1f, Raron (Valais) UL 2x; Saillon (Valais) UL 1x.

**BO-BOHEMIA:** Běleč (Hradec Králové) ASB 1f, Benešov nad Černou (Český Krumlov) ISZ 2m; Beroun (Beroun) ISZ 4f, Český Dub (Liberec) ISZ 2x, Dobruška (Hradec Králové) ASB 1m; Dobrušovice (Praha-západ) ISZ 30f, 1x; Dobruška (Příbram) ISZ 2m, 8f; Domažlice (Domažlice) ISZ 8m, 16f; Dvůr Králové (Trutnov) ASB 5f, Hlavice (Liberec) ISZ 1x; Hradec Králové (Hradec Králové) ASB 1m, Jaroměř (Náchod) ISZ 1f, Jemniště (Benešov) ISZ 1f, Jeseníky Mts. (undefined) ISZ 1m, 1f, Jilové u Prahy (Praha-západ) ISZ 2m, 7f, 2x; Kadov (Strakonice) ASB 1f; Kardašova Řečice (Jindřichův Hradec) NMP 2f; Karlštejn (Beroun) ISZ 7m, 8f, 1x, ASB 1m, 1f; Kašperské Hory (Klatovy) ASB 2f, Kolín (Kolín) ISZ 1m, Krušné hory Mts. (undefined) ISZ 1f; Ledce (Mladá Boleslav) ISZ 2m, 1f; Lnáře (Strakonice) ASB 1m; Malá Morávka (Bruntál) ASB 2m, 2f; Mořina (Beroun) ISZ 2f; Pecka (Jičín) ASB 1f, Pěčice (Mladá Boleslav) ISZ 1m, Perlejn (Chomutov) ISZ 1x, Píštěn (České Budějovice) ASB 2m, 2f, Pozdeň (Kladno) ISZ 1x, Praha (Praha) NMP 13f, 1x; Rabi (Klatovy) ISZ 6m, 3f; Rataje (Čáslav) ISZ 1f; Sedlec (České Budějovice) ASB 1m, 1f; Sněžné (Rychnov nad Kněžnou) ASB 1f, Srbsko (Beroun) ISZ 3m, 21f, 12x, ASB 6m, 7f, Stěžery (Hradec Králové) ASB 1f, Stráž nad Nežárkou (Jindřichův Hradec) ISZ 2f, Troja (Praha) ISZ 1m, 1x, Treboň (Jindřichův Hradec) ISZ 5m, 16f, 5x, Ústí nad Labem (Ústí nad Labem) ISZ 4f; Velký Týšský fishpond (Jindřichův Hradec) ISZ 1m, 3f, Vřesce (Tábor) ISZ 2f, Zbraslav (Praha) ISZ 7f, Zvíkov (Písek) ISZ 1m, 2f, 1x; Žinkovy (Plzeň-jih) ISZ 1m, Žofín (Český Krumlov) ISZ 1m

**MO-MORAVIA:** Blansko (Blansko) ASB 2f, Brno (Brno) ASB 3f, Byčí skála cave (Blansko) 4m, 13f, Černá Hora (Blansko) ASB 20f, Frenštát pod Radhoštěm (Nový Jičín) ASB 1f; Květnice u Tišnova (Brno-venkov) ASB 1m, Ledečko

(Všetín) ISZ 1m, Lomnice u Třnova (Blansko) ASB 5f, Macocha cave (Blansko) ASB 4m, 5f, Mikulov (Břeclav) ASB 1m, Moravský Krumlov (Znojmo) ASB 5f, Rájec nad Svitavou (Blansko) ASB 4f, Sádek (Třebíč) ISZ 1m, 1f, Sloupka cave (Blansko) ISZ 1m, ASB 2m, Radkov (Svitavy) ISZ 1m, Třnov (Brno-venkov) ASB 1f, Valašské Klobouky (Zlín) ISZ 3f, Valtice (Břeclav) ISZ 1m, ASB 1m, Veverí (Brno-venkov) ASB 2f, Žitár nad Sázavou (Žďár nad Sázavou) ASB 1f

**SK-SLOVAKIA:** Ardovo (Rožňava) ISZ 2m, 5f, Chlába (Nové Zámky) ISZ 2f, ASB 2m, 3f, Domica (Rožňava) NMP 3m, 6f, ASB 5m, 5f, Drienovec (Košice-vidiek) ISZ 1f, ASB 1f, Dražia cave (Liptovský Mikuláš) ISZ 5f, Dubnica nad Váhom (Povážská Bystrica) ISZ 4f, Hačava (Košice-vidiek) ISZ 1m, 1f, Harmanec (Banská Bystrica) ISZ 17m, 9f, ASB 2m, 1f, Ladzianskeho cave (Banská Bystrica) ISZ 2m, 1f, Liskovská cave (Liptovský Mikuláš) ASB 1f, Ludmíla cave (Rožňava) ISZ 2m, Slovakian karst (undefined) ISZ 2m, 7f, Tisovec (Rimavská Sobota) ISZ 1m, 1f, Veľké Leváre (Senica) ASB 4f, Zuberec (Dolný Kubín) ASB 1f

**PL-POLAND:** Nietoperek (Gorzów Wielkopolski) PB 2m, 4f, 2x

**BG-BULGARIA:** Bačkov (Plovdiv) ISZ 3m, 1f, 1x, Brestnica (Loveč) ISZ 9m, 1f, Bulgaria (undefined) ISZ 1x, ASB 1m, Čepelare (Smoljan) NMP 1f, Hajduška cave (Loveč) ISZ 4m, 1f, Jagodina (Smoljan) NMP 1m, Karlukovo (Loveč) ISZ 6m, 5f, ASB 1m, 1f, Komunari (Varna) ISZ 1m, Nova cave (Pazardžik) ISZ 1m, 1f, ASB 2m, 2f, Orehovo (Smoljan) ISZ 1m, Panežka cave (Loveč) ISZ 2m, 2f, Plöski (Sandanski) ISZ 4m, Prochodna cave (Loveč) ISZ 2m, 2f, Snežanka cave (Pazardžik) ISZ 4m, Spahievo (Haskovo) ISZ 3m, Suhata cave (Vraca) ISZ 1m, 4f, Temnata cave (Vraca) ISZ 5m, 1f, ASB 2f

**AL-ALBANIA:** Mezhgoranit cave (Tepelene) ISZ 4m, 7f, Vanista (Gjrokastrë) ISZ 3m, 1f

**GR-GREECE:** Greece (undefined) ISZ 2m, Kimmeria (Xanthi) ISZ 4m, 1f, Olympos (Pieria) ISZ 1f

**WT-WEST TURKEY:** Toros Mts (undefined) UL 1f, 1x

**ET-EAST TURKEY:** Akcaabat (Trabzon) AUV 1f, Camlımagara (Erzurum) AUV 4x, Karadut (Adıyaman) JO 2x

### *Myotis blythi*

**SP-SPAIN:** Barcelona (Cataluña) UL 1f

**SW-SWITZERLAND:** Folly (Valais) UL 2m, 1f, 2x, Lutry (Vaud) UL 1x, Naters (Valais) UL 1m, 2f, 2x, Rarogne (Valais) UL 1x, Raron (Valais) UL 4x

**MO-MORAVIA:** Byčí skála cave (Blansko) ASB 1f, Javoříčko (Olomouc) ASB 1f, Josefov (Blansko) ASB 1m, Lednice (Břeclav) ASB 1f, Macocha cave (Blansko) ASB 1m, Mikulov (Břeclav) ASB 1m, 1f, Ochozská cave (Brno-venkov) ASB 1f, Sloupka cave (Blansko) ISZ 2m

**SK-SLOVAKIA:** Bystrá pod Ďumbierom (Banská Bystrica) ISZ 2x, Červená Skala (Banská Bystrica) ASB 1m, 1f, Chlába (Nové Zámky) ISZ 2f, ASB 1f, Drienovec (Košice-vidiek) ISZ 3m, 1f, ASB 1f, Hačavská cave (Košice-vidiek) ISZ 4m, 5f, Harmanec (Banská Bystrica) ISZ 26m, 25f, 3x, ASB 1m, 2f, Hrhov (Rožňava) ISZ 1f, Liskovská cave (Liptovský Mikuláš) ASB 1m, 2f, Myto pod Ďumbierom (Banská Bystrica) ISZ 1m, 2f, Nizké Tatry Mts (undefined) ISZ 1m, ASB 1m, Plavecké Podhradie (Senica) ASB 4f, Slovakian karst (Rožňava) ISZ 1m, 2f, Trnec Mts (undefined) ASB 1f, Veľké Leváre (Senica) ASB 2f

**BG-BULGARIA:** Beloslav (Varna) NMP 1m, Bulgaria (undefined) ASB 2m, Gela (Smoljan) NMP 1m, Kamen Brjag (Tolbuhin) ISZ 2m, 2f, Karlukovo (Loveč) ISZ 2m, 1f, Mala Deška (Burgas) ISZ 1m, Maslen Nos (Burgas) ISZ 4m, 16f, 1x, Sliven (Sliven) ISZ 2m, NMP 1m

**AL-ALBANIA:** Mezhgoranit cave (Tepelene) ISZ 2m, 5f

**RO-ROMANIA:** Dobrugea (undefined) ISZ 2f, Cave Liliacilor de la Gura Dobrogei (Constanta) ISZ 1m, Cave de la Adam (Constanta) ISZ 1m

**WT-WEST TURKEY:** Erdek (Balıkesir) AUV 1m, 4f

**ET-EAST TURKEY:** Camlımagara (Erzurum) AUV 2x, Muradiye (Van) PB 1m, Tuzluca (Kars) AUV 5m, 2f, Van (Van) PB 4m, Karadut (Adıyaman) JO 10x

**TC-TRANSCAUCASIA:** Georgia T'bilisi (T'bilisi) ISZ 2m, Armenia Yerevan (Yerevan) ISZ 1m, 2x, Azerbaijan Kys Kalasy (Sheinakha) ISZ 6m, 7x

**NI-NORTH IRAN:** Mazdooran (Mashhad) AUV 6x

**TK-TURKMENISTAN:** Bakhardenskaya cave (Ahal) ISZ 7m, 12f, 1x

**UZ-UZBEKISTAN:** Amanicutan (Samarkand) ISZ 4m, Samarkand (Samarkand) ISZ 1m, 1f

**NK-NORTH KYRGYZSTAN:** Nizhnaya Serafimovka, Solyanka cave (Chuy) ISZ 9m, 5f

**KI-SOUTH KYRGYZSTAN:** Adzhidaar Ungur cave (Osh) ISZ 21m, 23f, Aravan (Osh) ISZ 1m, 1f, Barytovaya cave (Osh) ISZ 8m, 7f, Kara-Gol (Osh) ISZ 1f, Suleyman hill (Osh) ISZ 1m, Sasyk-Ungur caves (Osh) ISZ 2m, 1f, Tuya-Muyen chasni cave (Osh) ISZ 12m, 10f

## *Myotis nattereri* group

**NA-NORTH AFRICA:** Morocco Khenifra MHNP 1m, Algeria Aokas cave (Bejaia) MUB 1f, Ain Fezza (Tlemcen) PAS 12m, 6f

**SP-SPAIN:** Portugal Portugal (undefined) SMF 1f, Spain Linares (Andalucía) SMF 1f, Spain (undefined) BMNH 1x, Salamanca (Castilla a León) SMF 1m, WI 1m

**BO-BOHEMIA:** Beroun (Beroun) ISZ 1f, Bohemia (undefined) ISZ 3m, 1f, 8x, ZCM 1f, Chynovská cave (Tábor) ISZ 1m, 1f, Dvohřbět (Třeboň) ISZ 2f, 1x, Jilové u Prahy (Praha-západ) ISZ 1m, 1f, Kobyla (Beroun) ISZ 1f, Kozolupy (Beroun) ISZ 1m, Ovesné Kladruby (Třeboň) ISZ 1m, 1f, Srbsko (Beroun) ISZ 2m, Tměný Ujezd (Beroun) ISZ 1m, Týnčany (Příbram) ISZ 1m, Velký Tisy (Jindřichův Hradec) ISZ 2m, 8f 1x West Bohemia, more localities WMP 3m 6f

**MO-MORAVIA:** Hlavenice (Opava), Nový Dvůr (Opava), Na Pomezí cave (Šumperk) SMO 2m, 14f

**PL-POLAND:** Białowieża (Białystok) ZBS 1m, Konin (Konin) ZBS 1x, Lublin (Lublin) ZBS 8x, Nietoperek (Gorzów Wielkopolski) ZBS 2f, Poznań (Poznań) ZBS 3x, Wyszynice (Biała Podlaska) ZBS 1x

**SK-SLOVAKIA:** Bukova (Trenčín) SNMB 2m, Silecká laduica cave (Rožňava) WMP 1m, Dobútska cave (Správká Nová Ves) ISZ 1x

**BG-BULGARIA:** Breznica (Blagoevgrad) ISZ 3m, 1f, Karlukovo (Loveč) ISZ 2m, Gela, Jagodina, Rodopi Mts (Smoljan) ISZ 14m, 2f, Razlog (Blagoevgrad) ISZ 1m

**GR-GREECE:** Misras, Aokas (Peloponnesos peninsula) WI 3m, 16f

**WT-WEST TURKEY:** Alanya (Alanya) WI 1m, Seddülbahir (Canakkale) NMW 7f, Incekum (Alanya) WI 1m, 9f

**KD-KURDISTAN:** NE-Iraq, data taken from Rzebik-Kowalska et al (1978), material has been reexamined by one of us (JH), PAS 5

**TC-TRANSCAUCASIA:** Russia Dagestan (undefined) ZMU 1m, Armenia Yelenovka (Sevan Lake) ZIY 1m, Azerbaijan Tug (Gadrud) ISZ 1m, 2f, Kys-Kalasy (Shemakha) ISZ 1f

**TK-TURKMENISTAN:** Tschali (Kopet Mts) ZMU 2f, 2x, (incl type of *tschaliensis* Kuzynin, 1935) ZMU 1x

**IS-ISRAEL:** Sheik Abrak TAU 3f, Dor TAU 2f, Mt Carmel (type of *hovei* Harrison, 1964) BMNH 1f, Mt Carmel SMF 1f, Judea SMF 1x

**NI-NW Iran and SE Armenia:** Amagi (Arax valley), Armenia (type serie of *araxensis* Dahl, 1947) ZIY 2x, ISZ 1, Kutur-Su, North West Iran BMNH 2x.

## APPENDIX II LIST OF ABBREVIATIONS

### (a) Measurements

LCr = greatest length of skull  
 LCb = condylobasal length  
 LaZ = zygomatic breadth  
 Lai = interorbital breadth  
 Lalnf = *infraorbital breadth (between foramina infraorbitalia)*  
 LaN = breadth of braincase  
 LaM = mastoidal breadth (between *processi mastoidei*)  
 VN = height of braincase  
 VN2 = height of skull (with *bullae tympanicae*)  
 I1/M3/, C-M3/, P4-M3/, M1/M3/, M1-M2/, C-P4/, P2-P3/ = lengths of upper toothrow delimited with mesial and distal margins of the respective teeth  
 C-C P4-P4/, M3/M3/ = palatal distances between outer margins of respective teeth  
 LMd = length of mandible  
 CrH = height of *ramus mandibulae*  
 I1-M/3, C-M/3, P4-M/3, M1-M/3, C-P/4, P2-P/4, C-M/1, P4-M/1, M1-M/2 = lengths of lower toothrow delimited with mesial and distal margins of the respective teeth  
 P4a = length of P4  
 P4b = width of P4

(b) Collections:

**ASB** (IVZ) = Institute of Landscape Ecology, Academy of Sciences of Czech Republic, Brno, Czech Republic; **AUW** = Department of Zoology, Agricultural University, Vienna, Austria; **BMNH** = British Museum (Natural History), London, United Kingdom; **ISZ** = Department of Zoology, Charles University, Prague, Czech Republic; **JO** = private collection of Jolán Obuch, Nečpaly, Slovakia; **MG** = Museum Genève, Switzerland; **MHNP** = Muséum Hist. Nat. Paris, France; **MUB** = Department of Zoology and Ecology, Masaryk University, Brno, Czech Republic; **NMP** = Zoological collections, National Museum, Prague, Czech Republic; **NMW** = Zoological Collections, Museum of Natural History, Vienna, Austria; **PAS** = Institute of Systematic and Experimental Zoology PAS Krakow, Poland; **PB** = private collection of Petr Benda, Prague, Czech Republic; **SMF** = Natur Museum u. Forschungsinstitut Senckenberg, Frankfurt a.M., Germany; **SMO** = Silesian Museum, Opava, Czech Republic; **SNMB** = Zoological Collections, Slovakian National Museum, Bratislava, Slovakia; **TAU** = Department of Zoology, University of Tel Aviv, Israel; **UL** = Institute of Zoology and Ecology of Animals, University of Lausanne, Switzerland; **WI** = private collection of Willi Issel, Augsburg, Germany; **WMP** = West Bohemian Museum, Plzeň, Czech Republic; **ZBS** = Mammal Research Institute PAS, Białowieża, Poland; **ZIV** = Zoological Institute AS of Armenia, Yerevan; **ZMU** = Institute of Zoology, University of Moscow, Moscow, Russia.

(c) Samples:

**AL** - Albania, **BG** - Bulgaria, **BO** - Bohemia, **ET** - Eastern Turkey, **GR** - Greece, **IS** - Israel, **KD** - Kurdistan (NE Iraq), **KI** - Southern Kyrgyzstan, **MO** - Moravia, **NA** - Northern Africa (Morocco, Algeria, Tunisia), **NI** - Northern Iran (NW-Iran and SE Armenia in case of *M. nattereri* group), **NK** - Northern Kyrgyzstan, **PL** - Poland, **RO** - Romania, **SK** - Slovakia, **SP** - Spain (incl. Portugal), **SW** - Switzerland, **TC** - Transcaucasia (Azerbaijan, Armenia, Georgia, Dagestan), **TK** - Turkmenistan, **WT** - Western Turkey. See Fig. 1 and Appendix 1 for details.

## APPENDIX III - SURVEY OF BIOMETRIC DATA

*Myotis myotis*

Bohemia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	241	20.7	24.62	23.85	0.587	54	21.5	24.42	23.388	0.615	158	21.87	24.62	23.628	0.487	789	22.15	24.62	23.66	0.479
LCb	238	20.3	23.52	22.296	0.536	54	20.35	23.52	22.133	0.646	157	20.65	23.43	22.348	0.458	789	20.65	23.52	22.384	0.48
La2	235	13.5	15.95	14.942	0.407	47	13.5	15.87	14.86	0.48	151	13.62	15.75	14.943	0.373	778	13.5	15.95	14.989	0.401
Lal	277	4.57	5.8	5.22	0.179	62	4.57	5.8	5.243	0.2	181	4.68	5.65	5.204	0.17	212	4.57	5.65	5.23	0.17
Laluf	276	5.13	6.76	6.176	0.227	61	5.55	6.55	6.182	0.225	181	5.13	6.76	6.173	0.218	211	5.55	6.76	6.215	0.202
LaN	275	9.1	10.62	10.063	0.243	61	9.37	10.57	10.059	0.257	181	9.37	10.62	10.062	0.236	211	9.45	10.62	10.091	0.223
LaM	217	9.9	11.75	10.961	0.295	47	9.9	11.4	10.831	0.331	147	10.08	11.75	10.913	0.287	775	10.08	11.75	10.934	0.275
YN	252	6.4	8.7	7.995	0.307	35	7	8.4	7.922	0.301	164	7.2	8.7	8.029	0.26	195	7.2	8.7	8.045	0.253
YN2	174	7.85	10.5	9.659	0.394	40	8.65	10.4	9.654	0.412	111	8.7	10.4	9.657	0.333	172	8.75	10.5	9.747	0.316
Moravia and Slovakia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	265	10.25	12.32	11.484	0.304	58	10.52	12	11.439	0.328	173	10.45	12.15	11.507	0.285	204	10.45	12.32	11.53	0.281
C-M3	271	8.7	10.64	9.861	0.271	60	8.92	10.43	9.84	0.314	176	8.95	10.38	9.876	0.24	207	9	10.64	9.986	0.243
Pa-M3	277	6.2	7.65	7.177	0.193	60	6	7.65	7.164	0.194	182	6.45	7.55	7.187	0.184	212	6	7.65	7.281	0.171
M1-M3	275	5	4.75	5.778	0.212	60	3.55	6.1	5.79	0.176	181	5	6.75	5.77	0.231	212	5	6.75	5.77	0.224
C-P4	272	3.25	4.78	4.371	0.182	62	3.25	4.72	4.333	0.243	175	3.9	4.72	4.385	0.15	205	3.9	4.78	4.4	0.15
P2-P3	268	1.1	1.77	1.482	0.098	58	1.19	1.7	1.495	0.093	173	1.1	1.77	1.482	0.099	206	1.1	1.7	1.474	0.102
C-C	260	5.15	6.78	6.231	0.26	59	5.15	6.78	6.198	0.32	168	5.45	6.7	6.231	0.238	197	5.7	6.78	6.283	0.205
Pa-P4	272	6.45	8.25	7.676	0.271	60	6.45	8.25	7.685	0.35	179	6.87	8.17	7.687	0.251	206	6.45	8.25	7.724	0.232
M3-M5	272	8.55	10.6	9.869	0.323	58	8.85	10.6	9.881	0.324	180	8.55	10.55	9.889	0.331	207	8.55	10.6	9.937	0.284
Moravia and Slovakia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	176	21.52	25.02	23.894	0.568	57	21.52	24.92	23.831	0.699	119	21.7	25.02	23.931	0.526	156	21.52	25.02	23.957	0.513
LCb	174	20.55	23.72	22.651	0.522	52	20.64	23.72	22.613	0.619	115	20.55	23.63	22.685	0.484	154	20.64	23.72	22.713	0.465
La2	164	13.72	15.93	15.114	0.359	46	13.72	15.95	15.115	0.402	117	13.82	15.75	15.124	0.344	146	13.72	15.95	15.126	0.352
Lal	187	4.85	5.85	5.219	0.159	57	4.9	5.85	5.244	0.182	124	4.85	5.65	5.213	0.148	166	4.85	5.65	5.236	0.153
Laluf	189	5.01	6.95	6.283	0.267	57	5.01	6.85	6.267	0.319	124	5.2	6.95	6.283	0.246	168	5.22	6.95	6.298	0.234
LaN	181	9.52	10.63	10.103	0.208	57	9.73	10.6	10.091	0.2	127	9.52	10.63	10.114	0.211	160	9.52	10.63	10.103	0.205
LaM	165	10.1	11.5	10.991	0.269	48	10.25	11.45	10.939	0.254	115	10.2	11.5	11.013	0.275	144	10.2	11.5	11.008	0.257
YN	177	7.28	9.05	8.175	0.271	57	7.45	9.05	8.154	0.295	119	7.28	8.83	8.187	0.221	157	7.45	8.83	8.18	0.258
YN2	128	8.9	10.3	9.912	0.292	40	9.05	10.45	9.907	0.31	85	8.9	10.3	9.914	0.285	111	9.05	10.45	9.927	0.277
Moravia and Slovakia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	180	10.47	12.27	11.654	0.284	57	10.47	12.23	11.628	0.347	121	10.53	12.27	11.642	0.258	159	10.47	12.27	11.681	0.262
C-M3	176	8.33	10.52	9.895	0.239	57	9.08	10.4	9.891	0.279	123	8.93	10.52	10.067	0.219	155	9.08	10.52	10.067	0.229
Pa-M3	189	6.5	7.65	7.281	0.176	57	6.55	7.5	7.238	0.195	124	6.5	7.65	7.348	0.162	168	6.55	7.65	7.384	0.172
M1-M3	189	5.23	6.3	5.886	0.167	57	5.28	6.17	5.848	0.187	124	5.32	6.3	5.947	0.153	168	5.28	6.3	5.887	0.166
C-P4	178	3.9	4.95	4.467	0.158	57	4.02	4.83	4.439	0.176	123	3.9	4.95	4.468	0.151	157	4.02	4.95	4.478	0.153
P2-P3	178	1	1.4	1.582	0.103	57	1	1.8	1.494	0.126	121	1.32	1.8	1.597	0.092	157	1	1.8	1.499	0.098
C-C	169	5.35	6.85	6.327	0.22	57	5.55	6.8	6.344	0.259	116	5.67	6.85	6.338	0.2	150	5.7	6.85	6.383	0.194
Pa-P4	189	6.95	8.43	7.8	0.258	57	7.1	8.25	7.745	0.297	124	6.95	8.43	7.829	0.231	168	7.02	8.43	7.82	0.245
M3-M5	146	8.62	10.77	10.008	0.317	57	8.62	10.45	9.822	0.386	124	9.12	10.77	10.051	0.277	160	9.2	10.77	10.033	0.28
Moravia and Slovakia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	194	16.05	19.3	18.196	0.446	57	16.05	19.05	18.14	0.518	124	16.17	19.3	18.232	0.419	156	16.35	19.3	18.245	0.421
C-H	190	5.3	6.6	6.107	0.244	57	5.35	6.58	6.182	0.261	124	5.3	6.58	6.11	0.237	156	5.35	6.58	6.117	0.229
U1-M3	174	11	13	12.319	0.282	57	11	12.8	12.383	0.353	123	11.05	13	12.339	0.254	156	11	13	12.339	0.267
C-M3	179	9.57	11.35	10.795	0.264	57	9.57	11.25	10.765	0.318	124	9.72	11.35	10.807	0.244	156	9.57	11.35	10.807	0.258
P4-M3	185	7.07	8.47	8.056	0.214	57	7.07	8.35	8.097	0.241	124	7.09	8.47	8.087	0.193	156	7.07	8.47	8.065	0.203
M1-M3	184	5.78	6.92	6.334	0.16	57	5.78	6.8	6.491	0.181	123	5.85	6.92	6.386	0.151	156	5.78	6.9	6.392	0.154
C-P4	179	3.9	4.91	4.496	0.163	57	3.95	4.85	4.487	0.19	124	3.9	4.91	4.501	0.152	156	3.98	4.93	4.508	0.155
P2-P4	179	2.65	3.35	3.146	0.151	57	2.65	3.42	3.163	0.162	124	2.7	3.35	3.148	0.146	156	2.65	3.35	3.177	0.149



# Balkan

	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	55	20.97	24.95	23.767	0.669	57	21.51	24.95	23.78	0.668	35	20.97	24.85	23.738	0.693	67	20.97	24.82	23.853	0.585
LCb	92	19.97	23.45	22.573	0.629	55	20.21	23.45	22.591	0.657	54	19.90	23.18	22.537	0.613	66	19.97	23.45	22.653	0.55
LaZ	89	13.7	15.75	15.039	0.4	54	13.83	15.75	15.054	0.427	52	13.7	15.45	15.048	0.371	60	13.7	15.75	15.106	0.353
LaI	96	4.85	5.65	5.152	0.162	58	4.88	5.65	5.191	0.15	35	4.85	5.53	5.062	0.164	67	4.87	5.65	5.15	0.156
LaInf	98	3.47	6.63	6.099	0.226	58	3.47	6.63	6.14	0.239	35	3.5	6.44	6.036	0.222	67	3.6	6.63	6.149	0.2
LaN	97	9.47	10.61	10.005	0.318	59	9.7	10.61	10.044	0.215	35	9.47	10.4	9.968	0.264	68	9.55	10.55	10.048	0.2
LaM	90	9.48	11.4	10.002	0.315	59	10.02	11.4	10.536	0.27	35	9.48	11.14	10.772	0.38	68	9.48	11.4	10.864	0.278
VN	97	7.37	8.72	8.128	0.248	59	7.37	8.7	8.139	0.235	29	7.45	8.32	8.099	0.256	68	7.57	8.72	8.178	0.22
VN2	72	8.45	10.67	9.917	0.301	57	8.85	10.67	9.935	0.344	34	9.6	10.5	9.914	0.213	50	8.85	10.67	9.967	0.296
II-M3/	94	10.55	12.23	11.695	0.31	57	10.65	12.23	11.698	0.323	35	10.55	12.23	11.698	0.299	67	10.55	12.23	11.71	0.304
C-M3/	98	8.72	10.55	10.014	0.327	58	8.72	10.55	10.081	0.31	35	8.8	10.42	10.031	0.297	67	8.8	10.55	10.044	0.298
PA-M3/	92	6.37	7.55	7.235	0.226	59	6.37	7.55	7.234	0.235	35	6.45	7.55	7.246	0.216	68	6.45	7.55	7.245	0.206
M1-M3/	97	5.22	6.28	5.826	0.184	59	5.25	6.12	5.793	0.186	35	5.22	6.28	5.84	0.177	68	5.22	6.12	5.818	0.171
C-P4/	90	3.8	4.85	4.487	0.19	58	3.8	4.85	4.487	0.199	35	4	4.75	4.473	0.172	67	4	4.85	4.533	0.143
P2-P3/	90	1.11	1.67	1.493	0.108	58	1.11	1.67	1.489	0.115	35	1.2	1.67	1.499	0.1	67	1.2	1.67	1.483	0.105
C-C	96	5.25	6.55	6.201	0.216	58	5.25	6.55	6.207	0.229	35	5.74	6.52	6.174	0.196	67	5.75	6.55	6.241	0.175
PA-P4/	90	6.82	8.13	7.65	0.26	58	6.82	8.13	7.658	0.276	35	6.80	8.07	7.634	0.245	67	6.87	8.13	7.686	0.23
M3-M3/	93	8.75	10.38	9.826	0.33	55	8.87	10.38	9.825	0.331	35	8.75	10.3	9.818	0.343	65	9.05	10.38	9.875	0.286
LMd	97	16.05	18.87	18.07	0.497	59	16.33	18.87	18.058	0.515	35	16.05	18.85	18.082	0.491	68	16.05	18.8	18.116	0.44
CrH	97	5	6.8	6.154	0.302	59	5.1	6.8	6.163	0.318	35	5	6.6	6.151	0.286	68	5	6.8	6.2	0.271
I/I-M3/	97	10.77	12.9	12.292	0.346	59	10.77	12.9	12.265	0.364	35	11.12	12.87	12.527	0.317	68	11.12	12.9	12.316	0.3
C-M3/	97	9.37	11.92	10.798	0.376	59	9.37	11.9	10.759	0.395	35	9.68	11.92	10.857	0.354	68	9.68	11.92	10.815	0.361
P4-M3/	90	6.87	8.4	8.61	0.245	59	6.87	8.4	7.978	0.279	34	7.2	8.37	8.067	0.269	67	7.25	8.4	7.977	0.216
M/I-M3/	97	5.72	6.78	6.481	0.2	59	5.78	6.78	6.465	0.204	35	5.72	6.78	6.587	0.191	68	5.72	6.78	6.472	0.189
C-P4/	97	3.82	4.83	4.543	0.193	59	3.82	4.83	4.543	0.199	35	4.03	4.8	4.537	0.180	68	4.03	4.83	4.557	0.177
P2-P4/	97	2.6	3.6	3.221	0.175	59	2.6	3.55	3.203	0.177	35	2.82	3.6	3.242	0.163	68	2.82	3.6	3.237	0.156

# N-Africa

	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	72	21.2	23.37	22.073	0.433	47	21.2	23.37	22.125	0.427	25	21.25	22.91	21.976	0.436	70	21.2	22.92	22.059	0.409
LCb	72	19.88	22.48	20.995	0.432	46	20.08	22.48	21.024	0.424	25	19.88	21.71	20.942	0.45	69	19.88	21.71	20.973	0.399
LaZ	65	13.4	14.98	14.153	0.302	47	13.55	14.98	14.234	0.282	24	13.4	14.52	14.014	0.268	67	13.4	14.98	14.14	0.295
LaI	72	4.82	5.51	5.153	0.158	47	4.83	5.51	5.178	0.145	25	4.82	5.48	5.106	0.173	70	4.82	5.51	5.152	0.16
LaInf	72	3.52	6.05	5.616	0.176	47	3.53	6.05	5.655	0.173	25	3.52	5.88	5.544	0.161	70	3.52	6.05	5.613	0.176
LaN	72	9.53	10.24	9.763	0.199	47	9.53	10.24	9.808	0.202	25	9.42	10.08	9.678	0.164	70	9.53	10.17	9.755	0.193
LaM	72	9.95	10.92	10.463	0.193	47	9.95	10.92	10.489	0.198	25	10.05	10.76	10.393	0.181	70	9.95	10.76	10.427	0.186
VN	72	7.22	8.13	7.632	0.197	46	7.35	8.13	7.875	0.181	25	7.22	7.95	7.584	0.204	69	7.22	8.05	7.625	0.19
VN2	55	8.77	9.82	9.399	0.241	35	8.77	9.81	9.444	0.221	22	8.92	9.82	9.319	0.258	53	8.77	9.82	9.321	0.239
II-M3/	72	10.22	11.77	10.737	0.279	46	10.22	11.77	10.787	0.287	25	10.23	11.17	10.644	0.241	69	10.22	11.26	10.722	0.253
C-M3/	72	8.42	10.12	9.221	0.251	47	8.42	10.12	9.243	0.27	25	8.41	9.53	9.18	0.209	70	8.42	9.62	9.208	0.23
PA-M3/	72	6.13	7.35	6.58	0.182	47	6.18	7.35	6.591	0.203	25	6.27	6.8	6.559	0.134	70	6.18	6.95	6.569	0.159
M1-M3/	72	4.87	6.02	5.273	0.178	46	4.87	6.02	5.478	0.193	25	5.02	5.53	5.266	0.141	69	4.87	5.57	5.261	0.153
C-P4/	72	3.95	4.54	4.269	0.136	47	4.02	4.55	4.299	0.125	25	3.95	4.5	4.213	0.129	70	3.95	4.55	4.269	0.136
P2-P3/	72	1.2	1.56	1.375	0.083	47	1.2	1.52	1.383	0.08	22	1.24	1.56	1.36	0.087	70	1.2	1.56	1.373	0.083
C-C	68	5.37	5.97	5.616	0.158	44	5.37	5.97	5.665	0.161	24	5.37	5.73	5.534	0.107	67	5.37	5.97	5.616	0.159
PA-P4/	72	6.48	7.72	7.083	0.213	47	6.48	7.72	7.123	0.227	25	6.72	7.35	7.007	0.162	70	6.48	7.57	7.076	0.201
M3-M3/	72	8.47	10.12	9.075	0.287	47	8.68	10.12	9.116	0.262	25	8.47	9.92	9.098	0.305	70	8.47	9.92	9.065	0.253
LMd	72	15.77	17.82	16.652	0.344	47	16	17.82	16.706	0.33	25	15.77	17.17	16.55	0.353	70	15.77	17.37	16.635	0.319
CrH	72	5.21	6.12	5.712	0.205	47	5.23	6.12	5.723	0.216	25	5.21	6.08	5.693	0.185	70	5.21	6.12	5.709	0.206
I/I-M3/	72	10.79	12.33	11.33	0.26	47	10.79	12.33	11.387	0.281	25	10.95	11.7	11.279	0.211	70	10.79	11.78	11.319	0.233
C-M3/	72	9.35	10.88	9.945	0.261	46	9.35	10.88	9.974	0.283	25	9.52	10.35	9.891	0.207	69	9.35	10.42	9.933	0.238
P4-M3/	72	6.78	8.17	7.295	0.21	47	6.78	8.17	7.303	0.237	25	6.95	7.57	7.28	0.152	70	6.78	7.7	7.285	0.184
M/I-M3/	72	5.43	6.72	5.878	0.187	47	5.43	6.72	5.883	0.215	25	5.67	6.1	5.871	0.121	70	5.43	6.17	5.866	0.16
C-P4/	70	3.71	4.57	4.267	0.159	46	3.77	4.57	4.288	0.172	25	3.92	4.47	4.231	0.128	68	3.77	4.55	4.263	0.157
P2-P4/	72	2.7	3.32	3.021	0.141	47	2.72	3.32	3.047	0.134	25	2.7	3.27	2.972	0.141	70	2.7	3.32	3.018	0.141

Spain					Switzerland					Moravia					Slovakia					
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	2	23.25	23.85	23.55	0.424	16	21.28	24.05	23.243	0.747	82	22.18	25.02	23.918	0.403	94	21.52	24.02	23.873	0.625
LCb	2	22.15	22.6	22.375	0.318	16	19.88	23	22.939	0.787	81	20.97	23.56	22.474	0.429	97	20.35	23.72	22.632	0.593
LaZ	2	14.03	15.25	15.1	0.212	12	13.37	15.75	14.094	0.37	81	14	15.75	15.899	0.3	87	13.72	15.93	15.129	0.409
LaI	2	5.28	5.37	5.325	0.084	16	4.9	5.4	5.162	0.167	82	4.85	5.65	5.219	0.358	705	4.9	5.85	5.319	0.16
LaInI	2	5.85	6.05	5.95	0.141	16	5.28	6.3	5.95	0.258	82	5.67	6.95	6.365	0.214	707	5.01	6.85	6.219	0.286
LaN	2	10.18	10.35	10.268	0.12	28	9.37	10.72	10.021	0.303	82	9.55	10.65	10.1	0.199	99	9.52	10.6	10.188	0.210
LaM	2	11.05	11.1	11.075	0.039	78	9.82	11.15	10.754	0.391	82	10.2	11.5	11.054	0.234	81	10.25	11.47	10.928	0.287
YN	2	7.98	8	7.99	0.014	16	7.3	8.47	7.978	0.346	82	7.45	8.78	8.168	0.253	95	7.28	9.05	8.181	0.286
YN2	2	9.75	9.97	9.86	0.136	10	8.7	10.28	9.687	0.466	81	9.15	10.46	9.922	0.257	67	8.8	10.5	9.983	0.325
1V/MSI	2	11.33	11.7	11.515	0.252	78	10.2	12	11.45	0.448	82	10.78	12.15	11.619	0.214	98	10.47	12.27	11.684	0.35
C MSI	2	9.74	10	9.87	0.184	16	8.68	10.2	9.826	0.373	82	9.18	10.52	10.045	0.197	94	8.95	10.5	10.054	0.272
PI/MSI	2	6.87	7.02	6.945	0.106	16	6.32	7.3	7.142	0.273	82	6.87	7.6	7.278	0.14	707	6.5	7.63	7.232	0.199
MI/MSI	2	5.85	5.75	5.7	0.071	16	5.2	6.17	5.881	0.242	82	5.45	6.17	5.895	0.135	707	5.28	6.1	5.879	0.189
C PI	2	4.4	4.45	4.425	0.015	16	3.8	4.55	4.324	0.182	82	4	4.95	4.664	0.154	96	3.9	4.93	4.468	0.162
PI/PI	2	1.52	1.56	1.54	0.03	16	1.19	1.67	1.468	0.124	81	1.3	1.8	1.521	0.1	97	1	1.7	1.486	0.101
C C	2	6.1	6.37	6.235	0.191	16	5.47	6.35	6.089	0.33	77	6.03	6.83	6.363	0.169	92	5.55	6.7	6.296	0.252
PI/PI	2	7.6	7.85	7.725	0.177	16	6.8	8.1	7.523	0.356	82	7.45	8.43	7.866	0.205	707	6.93	8.32	7.75	0.283
MSI/MSI	2	10.08	10.12	10.1	0.028	16	8.63	10.4	9.822	0.461	82	9.3	10.77	10.077	0.263	104	8.62	10.6	9.954	0.346
LMd	2	17.5	18.1	17.8	0.474	16	15.7	18.62	17.711	0.71	82	16.75	19.05	18.244	0.35	772	16.03	19.1	18.161	0.503
CrH	2	5.92	5.92	5.92	0	16	4.95	6.47	5.887	0.403	82	5.63	6.58	6.157	0.202	714	5.3	6.6	6.071	0.286
1V MSI	2	11.65	12.28	12.065	0.304	16	10.6	12.62	12.039	0.465	82	11.56	12.82	12.323	0.221	96	11	13	12.318	0.326
C MSI	2	10.35	10.75	10.55	0.283	16	9.25	11.12	10.554	0.445	82	10.07	11.35	10.784	0.219	97	9.57	11.15	10.384	0.298
PI/MSI	2	7.52	7.82	7.67	0.213	16	6.83	8.45	7.934	0.398	82	7.57	8.82	8.072	0.159	707	7.09	8.47	8.044	0.25
MI/MSI	2	6.2	6.25	6.225	0.035	16	5.57	6.82	6.434	0.293	81	6.27	6.77	6.538	0.113	707	5.79	6.92	6.531	0.189
C PI	2	4.45	4.51	4.48	0.042	16	3.78	4.68	4.485	0.231	82	3.95	4.93	4.584	0.15	97	3.9	4.85	4.489	0.174
PI/PI	2	3.1	3.27	3.185	0.12	16	2.56	3.32	3.097	0.2	82	2.65	3.55	3.166	0.139	97	2.7	3.46	3.166	0.181
Poland					Bulgaria					Albania					Greece					
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	8	23	24.33	23.634	0.524	76	20.97	24.95	23.758	0.72	75	22.6	24.25	23.767	0.42	4	23.45	24.52	23.948	0.439
LCb	8	21.85	23	22.444	0.487	77	19.97	23.45	22.56	0.688	75	21.52	23.05	22.587	0.348	4	22.62	22.95	22.76	0.148
LaZ	8	14.55	15.87	15.19	0.406	70	13.7	15.75	15.022	0.424	75	14.56	15.6	15.116	0.302	4	14.6	15.35	15.055	0.321
LaI	8	4.98	5.38	5.186	0.153	77	4.85	5.65	5.164	0.159	75	4.88	5.37	5.113	0.158	4	4.85	5.38	5.075	0.24
LaInI	8	6.32	6.55	6.335	0.116	77	5.47	6.63	6.094	0.244	75	5.72	6.38	6.101	0.218	4	6.05	6.4	6.193	0.165
LaN	8	9.9	10.52	10.171	0.185	78	9.47	10.61	10.013	0.239	75	9.48	10.33	9.987	0.23	4	9.72	10.18	9.913	0.202
LaM	8	10.6	11.25	10.964	0.179	77	9.48	11.4	10.847	0.333	75	10.18	11.1	10.784	0.241	4	10.52	11.07	10.77	0.248
YN	8	7.88	8.5	8.138	0.293	78	7.37	8.7	8.115	0.258	75	7.8	8.4	8.144	0.165	4	8.13	8.72	8.338	0.261
YN2	8	9.8	10.4	10.092	0.198	86	8.85	10.67	9.9	0.32	77	9.6	10.2	9.969	0.19	3	9.82	10.25	10.073	0.225
1V/MSI	8	11.37	11.91	11.663	0.19	75	10.55	12.23	11.662	0.324	75	11.3	12.23	11.827	0.213	4	11.55	12	11.83	0.203
C MSI	8	9.72	10.43	10.099	0.238	77	8.72	10.55	9.98	0.348	75	9.73	10.38	10.149	0.175	4	9.97	10.37	10.153	0.187
PI/MSI	8	7.02	7.45	7.345	0.206	78	6.37	7.55	7.216	0.233	75	6.75	7.55	7.323	0.194	4	7.17	7.4	7.275	0.187
MI/MSI	8	5.72	6.05	5.871	0.13	78	5.22	6.28	5.806	0.193	75	5.7	6.08	5.921	0.117	4	5.75	5.97	5.858	0.098
C PI	8	4.34	4.68	4.498	0.139	77	3.8	4.85	4.462	0.195	75	4.32	4.77	4.57	0.128	4	4.52	4.81	4.648	0.142
PI/PI	8	1.43	1.61	1.486	0.063	77	1.11	1.66	1.483	0.113	75	1.41	1.67	1.535	0.08	4	1.48	1.59	1.533	0.051
C C	8	6.16	6.77	6.51	0.182	77	5.35	6.55	6.197	0.228	75	5.74	6.37	6.184	0.164	4	6.17	6.42	6.348	0.119
PI/PI	8	7.63	8.17	7.919	0.214	77	6.82	8.13	7.648	0.273	75	7.13	7.97	7.647	0.227	4	7.62	7.8	7.713	0.101
MSI/MSI	8	9.6	10.6	10.05	0.335	74	8.87	10.38	9.833	0.326	75	8.75	10.18	9.751	0.369	4	9.68	10.17	9.958	0.217
LMd	7	17.87	18.73	18.226	0.34	78	16.05	18.87	18.064	0.579	75	17.33	18.55	18.055	0.291	4	18.08	18.37	18.25	0.136
CrH	8	5.68	6.32	6.065	0.231	78	5	6.8	6.148	0.329	75	5.85	6.45	6.181	0.157	4	6	6.37	6.18	0.163
1V MSI	8	12.33	12.77	12.525	0.178	78	10.77	12.9	12.297	0.363	75	11.95	12.87	12.441	0.221	4	12.07	12.45	12.418	0.249
C MSI	8	10.52	11.2	10.851	0.253	78	9.37	11.9	10.767	0.368	75	9.97	11.92	10.941	0.434	4	10.65	11.02	10.88	0.164
PI/MSI	8	7.72	8.32	8.033	0.217	78	6.1	8.4	7.98	0.339	75	7.8	8.23	8.066	0.139	4	7.78	8.05	7.918	0.137
MI/MSI	8	6.25	6.75	6.504	0.196	78	5.72	6.78	6.47	0.212	75	6.25	6.72	6.549	0.14	4	6.35	6.57	6.455	0.1
C PI	8	4.23	4.68	4.544	0.151	78	3.82	4.82	4.516	0.195	75	4.3	4.83	4.643	0.149	4	4.52	4.82	4.703	0.131
PI/PI	8	2.92	3.48	3.221	0.17	78	2.6	3.6	3.192	0.175	75	3.12	3.48	3.313	0.12	4	3.35	3.58	3.453	0.101

		W-Turkey					E-Turkey				
		n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	2	23.37	23.56	23.475	0.146	✓	23.73	25.15	24.628	0.621	
LCb	2	22.48	22.78	22.6	0.17	✓	23.05	24.05	23.658	0.437	
LaZ	2	14.77	15.55	15.16	0.552	✓			15.25		
LaI	2	5.12	5.12	5.12	0	✓	5.07	5.37	5.2	0.115	
LaIaI	2	5.78	5.88	5.83	0.071	✓	5.97	6.52	6.25	0.225	
LaN	2	9.78	9.85	9.815	0.049	✓	9.78	10.43	10.195	0.266	
LaM	2	10.51	10.62	10.745	0.247	✓	11	11.05	11.915	0.021	
YN	2	8.11	8.31	8.21	0.127	✓	8.05	8.52	8.315	0.204	
YN2	2	9.8	10	9.9	0.141	✓			9.87		
II-M3/	2	11.35	11.77	11.76	0.014	✓			12.12		
C-M3/	2	10.07	10.12	10.095	0.015	✓			10.42		
PA-M3/	2	7.32	7.35	7.335	0.021	✓	7.15	7.58	7.378	0.155	
MI-M3/	2	5.77	5.82	5.895	0.077	✓	5.85	6.25	6.028	0.172	
C-P4/	2	4.4	4.58	4.49	0.127	✓			4.83		
P2-P4/	2	1.12	1.39	1.21	0.112	✓			1.56		
C-C	2	6.3	6.87	6.65	0.191	✓			6.38		
PA-M4/	2	7.72	7.92	7.82	0.141	✓	7.65	8.12	7.948	0.189	
M3-M3/	2	10.1	10.12	10.11	0.014	✓	9.95	10.5	10.15	0.282	
LM4	2	17.62	18.35	18.975	0.361	✓	18.88	19.22	19.05	0.24	
CrB	2	5.92	6.25	6.085	0.233	✓	6.37	6.53	6.45	0.113	
I/I-M3/	2	12.33	12.35	12.34	0.014	✓			12.57		
C-M3/	2	10.87	10.88	10.875	0.007	✓			11.13		
PA-M3/	2	8.05	8.17	8.11	0.085	✓			7.95		
MI-M4/	2	6.35	6.72	6.625	0.12	✓	6.52	7	6.76	0.139	
C-P4	2	4.57	4.61	4.59	0.025	✓			4.72		
P2-P4	2	3.1	3.16	3.13	0.042	✓			3.43		

### *Myotis blythi*

Moravia and Slovakia																				
	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	103	20.44	22.42	21.38	0.452	46	20.44	22.42	21.384	0.47	55	20.5	22.17	21.351	0.429	62	20.52	22.37	21.464	0.439
LCb	100	19.52	21.78	20.286	0.425	45	19.52	21.78	20.296	0.484	55	19.59	20.85	20.252	0.348	60	19.52	21.2	20.353	0.391
LaZ	80	12.88	14.22	13.648	0.312	37	13.17	14.22	13.692	0.278	42	12.88	14.2	13.597	0.329	48	13.15	14.2	13.712	0.259
LaI	103	4.65	5.62	5.115	0.19	46	4.65	5.62	5.164	0.171	55	4.68	5.42	5.065	0.191	62	4.65	5.62	5.116	0.184
LaIaI	103	4.93	6.05	5.423	0.214	46	5	6	5.479	0.208	55	4.93	6.05	5.373	0.211	62	4.93	6.05	5.437	0.215
LaN	103	8.88	10.08	9.614	0.214	46	9.15	9.97	9.651	0.173	55	8.88	10.04	9.575	0.238	62	8.88	10.02	9.632	0.218
LaM	101	9.25	10.57	10	0.253	45	9.47	10.57	10.018	0.237	54	9.25	10.52	9.975	0.265	61	9.6	10.52	10.055	0.215
YN	101	7.05	8	7.523	0.209	46	7.1	8	7.561	0.192	53	7.05	7.9	7.477	0.21	61	7.05	8	7.563	0.205
YN2	78	8.4	9.92	8.998	0.26	37	8.7	9.5	9.055	0.217	41	8.4	9.92	8.946	0.287	49	8.4	9.92	9.018	0.271
II-M3/	102	9.73	11	10.348	0.213	46	9.73	11	10.357	0.238	54	9.9	10.7	10.329	0.194	62	9.73	11	10.349	0.217
C-M3/	100	8.35	9.37	8.863	0.206	44	8.48	9.37	8.849	0.214	54	8.35	9.11	8.756	0.189	60	8.35	9.37	8.814	0.22
PA-M3/	107	6.08	6.83	6.372	0.141	46	6.13	6.72	6.38	0.144	55	6.08	6.83	6.346	0.14	62	6.08	6.83	6.375	0.149
MI-M3/	109	4.73	5.45	5.281	0.123	46	4.87	5.45	5.282	0.134	55	4.73	5.42	5.201	0.119	62	4.73	5.42	5.195	0.131
C-P4/	101	3.43	4.5	3.934	0.181	45	3.6	4.5	3.974	0.189	54	3.43	4.25	3.895	0.161	60	3.58	4.35	3.953	0.166
P2-P4/	101	1.04	1.41	1.285	0.069	45	1.04	1.41	1.286	0.064	54	1.04	1.33	1.197	0.073	62	1.04	1.33	1.196	0.066
C-C	48	5.15	6.22	5.684	0.165	44	5.4	6.22	5.715	0.169	52	5.15	6	5.676	0.164	58	5.15	6.22	5.693	0.153
PA-P4/	102	6.48	7.53	6.987	0.194	46	6.57	7.53	7.017	0.212	54	6.48	7.27	6.955	0.172	62	6.48	7.51	7.01	0.201
M3-M3/	103	8.35	9.92	8.875	0.275	46	8.35	9.4	8.879	0.283	55	8.36	9.92	8.86	0.27	63	8.35	9.92	8.923	0.282
LM4	103	15.32	17.72	16.287	0.416	46	15.6	17.72	16.271	0.449	54	15.32	16.93	16.135	0.38	62	15.32	16.93	16.219	0.385
CrB	100	4.67	6.02	5.2	0.2	45	4.75	5.63	5.281	0.181	52	4.67	6.02	5.191	0.217	60	4.75	5.63	5.287	0.181
I/I-M3/	101	10.3	11.4	10.85	0.243	45	10.45	11.4	10.872	0.238	54	10.3	11.3	10.819	0.244	61	10.3	11.4	10.854	0.255
C-M3/	102	8.4	10.2	9.468	0.222	46	9.18	10.2	9.581	0.213	54	8.6	9.92	9.431	0.227	62	8.4	10.02	9.472	0.225
PA-M3/	107	6.6	7.46	6.993	0.179	46	6.6	7.46	6.993	0.175	54	6.67	7.45	6.992	0.187	62	6.6	7.4	6.98	0.177
MI-M3/	103	5.37	6.12	5.705	0.134	46	5.4	6	5.782	0.137	54	5.37	6.13	5.706	0.129	62	5.37	6.13	5.695	0.141
C-P4	102	3.52	4.5	3.888	0.162	46	3.52	4.25	3.888	0.147	53	3.52	4.12	3.856	0.131	62	3.52	4.5	3.899	0.17
P2-P4	101	2.43	3.15	2.737	0.134	46	2.45	3.15	2.755	0.127	53	2.43	3.03	2.716	0.134	62	2.43	3.15	2.725	0.123



# Balkan

	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	43	20.35	22.35	21.346	0.477	22	20.57	22.1	21.324	0.455	20	20.35	22.35	21.364	0.521	32	20.57	22.05	21.395	0.426
LCb	40	19.15	21	20.326	0.456	22	19.55	21	20.306	0.435	17	19.15	20.97	20.251	0.507	22	19.54	21	20.271	0.403
LaZ	32	12.87	14.19	13.431	0.359	16	13.15	14.19	13.741	0.305	15	12.87	14.08	13.473	0.385	25	12.87	14.19	13.67	0.306
LaI	46	4.72	5.42	5.03	0.183	22	4.82	5.42	5.09	0.147	23	4.72	5.22	4.982	0.161	25	4.8	5.42	5.053	0.15
LaInf	47	4.95	5.92	5.453	0.196	23	5.2	5.92	5.525	0.168	23	4.95	5.9	5.394	0.2	25	5.17	5.92	5.486	0.169
LaN	64	9.2	10.22	9.58	0.215	22	9.4	10.22	9.596	0.2	21	9.2	9.97	9.556	0.235	23	9.21	10.22	9.596	0.219
LaM	43	9.27	10.28	9.886	0.223	23	9.58	10.28	9.937	0.196	19	9.27	10.25	9.82	0.244	23	9.55	10.28	9.94	0.165
VN	39	7.1	8.07	7.518	0.268	21	7.1	8.05	7.541	0.274	17	7.13	8.07	7.48	0.27	21	7.13	8.05	7.562	0.242
VN2	32	8.6	9.83	9.063	0.288	17	8.6	9.83	9.111	0.314	14	8.65	9.46	9.001	0.263	24	8.6	9.83	9.123	0.277
II-MQ	49	9.72	10.98	10.333	0.27	23	9.83	10.8	10.332	0.263	25	9.72	10.98	10.338	0.283	37	9.72	10.8	10.388	0.251
C-MQ	49	8.06	9.25	8.759	0.256	22	8.06	9.12	8.797	0.23	25	8.1	9.25	8.766	0.265	47	8.06	9.12	8.766	0.252
Pa-MQ	49	5.87	6.6	6.327	0.145	23	6.17	6.52	6.327	0.095	25	5.87	6.6	6.327	0.183	37	5.87	6.6	6.353	0.136
MI-MQ	49	4.74	5.4	5.123	0.147	23	4.77	5.37	5.181	0.128	23	4.74	5.4	5.141	0.163	37	4.74	5.4	5.13	0.153
C-P4	49	3.32	4.32	3.942	0.177	23	3.65	4.32	3.969	0.192	25	3.32	4.25	3.915	0.166	37	3.65	4.32	3.96	0.168
P2-P4	49	1.05	1.39	1.206	0.099	23	1.05	1.39	1.211	0.096	25	1.06	1.35	1.203	0.083	37	1.05	1.37	1.209	0.086
C-C	48	4.85	6.03	5.631	0.241	23	5.22	6.03	5.664	0.235	24	4.85	6	5.6	0.252	36	5.25	6.03	5.69	0.193
Pa-P4	48	6.28	7.35	6.924	0.262	23	6.28	7.35	6.951	0.262	24	6.41	7.27	6.889	0.25	36	6.32	7.35	6.988	0.228
MS-M3	47	7.54	9.32	8.743	0.348	23	8.05	9.32	8.81	0.333	23	7.54	9.27	8.676	0.363	43	8.05	9.32	8.854	0.261
LMd	50	15.23	17.15	16.156	0.417	23	15.63	17.15	16.27	0.407	28	15.25	16.81	16.077	0.416	38	15.3	17.15	16.325	0.386
CrH	47	4.53	5.92	5.097	0.277	22	4.73	5.6	5.171	0.236	24	4.53	5.92	5.025	0.309	25	4.65	5.92	5.177	0.237
I1-M3	50	10.27	11.47	10.928	0.238	23	10.54	11.47	10.958	0.213	26	10.27	11.4	10.924	0.265	38	10.27	11.47	10.94	0.231
C-M3	50	8.85	9.93	9.471	0.22	23	9.15	9.85	9.489	0.172	28	8.85	9.93	9.455	0.261	38	8.85	9.85	9.489	0.214
Pa-M3	50	6.5	7.42	7.027	0.201	23	6.62	7.25	7.011	0.157	26	6.5	7.42	7.043	0.238	38	6.5	7.42	7.02	0.211
MI-M3	50	5.27	5.95	5.714	0.156	23	5.55	5.85	5.7	0.09	28	5.27	5.95	5.725	0.174	38	5.27	5.95	5.797	0.137
C-P4	50	3.58	4.23	3.885	0.151	23	3.73	4.23	3.986	0.14	26	3.58	4.2	3.864	0.162	38	3.6	4.23	3.984	0.143
P2-P4	49	2.32	3.07	2.765	0.133	23	2.52	3.05	2.882	0.197	26	2.32	3.07	2.761	0.152	38	2.52	3.07	2.778	0.112

# S-Kyrgyzstan

	all specimens					males					females					adult specimens				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	85	20.2	22.47	21.021	0.389	46	20.28	22.47	21.069	0.423	39	20.2	22.02	20.965	0.341	64	20.2	22.47	21.065	0.399
LCb	82	19.28	21.32	19.984	0.376	45	19.29	21.32	20.058	0.406	37	19.28	20.62	19.894	0.317	62	19.28	21.32	20.046	0.38
LaZ	74	12.82	14.17	13.555	0.321	39	12.82	14.15	13.611	0.313	35	12.95	14.17	13.492	0.322	55	12.95	14.17	13.611	0.314
LaI	87	4.7	5.37	5.034	0.154	47	4.8	5.37	5.047	0.137	40	4.7	5.37	4.998	0.17	64	4.7	5.37	5.01	0.153
LaInf	87	5.03	6.02	5.641	0.204	47	5.27	6.02	5.696	0.189	40	5.03	5.92	5.577	0.205	64	5.13	6.02	5.664	0.2
LaN	87	9.12	9.93	9.55	0.178	47	9.13	9.98	9.574	0.163	40	9.12	9.95	9.523	0.171	64	9.12	9.95	9.558	0.17
LaM	87	9.35	10.37	9.874	0.213	47	9.35	10.32	9.916	0.222	40	9.35	10.37	9.825	0.193	64	9.4	10.37	9.932	0.189
VN	82	6.93	7.96	7.415	0.201	45	7	7.96	7.434	0.2	37	6.95	7.8	7.389	0.202	62	6.95	7.96	7.441	0.21
VN2	81	8.47	9.42	8.893	0.223	43	8.47	9.35	8.904	0.222	38	8.51	9.42	8.881	0.228	58	8.51	9.42	8.93	0.225
II-MQ	86	9.72	10.9	10.282	0.237	46	9.82	10.9	10.299	0.251	40	9.72	10.58	10.262	0.198	62	9.72	10.9	10.316	0.217
C-MQ	87	8.28	9.13	8.682	0.179	47	8.28	9.11	8.65	0.185	40	8.31	9.13	8.673	0.168	64	8.31	9.13	8.702	0.182
Pa-MQ	87	5.9	6.67	6.324	0.14	47	5.9	6.67	6.337	0.139	40	5.93	6.57	6.308	0.142	64	5.93	6.6	6.329	0.129
MI-MQ	87	4.91	5.48	5.211	0.127	47	4.91	5.48	5.197	0.133	40	4.91	5.47	5.219	0.12	64	4.91	5.47	5.283	0.122
C-P4	86	3.57	4.22	3.845	0.132	47	3.62	4.17	3.868	0.136	39	3.57	4.22	3.818	0.122	63	3.6	4.22	3.86	0.128
P2-P4	87	1	1.33	1.19	0.068	47	1.04	1.33	1.196	0.067	40	1	1.3	1.183	0.049	64	1.04	1.33	1.183	0.063
C-C	87	4.83	6.13	5.599	0.219	47	5.12	6.13	5.647	0.212	40	4.83	5.8	5.543	0.191	64	5.25	6.13	5.682	0.197
Pa-P4	87	6.38	7.52	7.053	0.239	47	6.38	7.52	7.064	0.26	40	6.58	7.47	7.041	0.214	64	6.6	7.52	7.1	0.232
MS-M3	87	8.04	9.63	8.8	0.239	47	8.08	9.33	8.82	0.248	40	8.18	9.63	8.776	0.291	64	8.22	9.63	8.863	0.265
LMd	87	15.08	16.97	16.007	0.345	47	15.08	16.97	16.034	0.381	40	15.5	16.63	15.976	0.299	64	15.08	16.97	16.049	0.348
CrH	87	4.67	5.62	5.069	0.176	47	4.7	5.62	5.092	0.181	40	4.67	5.4	5.043	0.169	64	4.8	5.62	5.101	0.163
I1-M3	86	10.37	11.42	10.89	0.217	46	10.52	11.42	10.908	0.214	40	10.37	11.22	10.878	0.222	62	10.38	11.42	10.894	0.221
C-M3	87	9.02	9.77	9.432	0.185	47	9.02	9.77	9.446	0.196	40	9.05	9.72	9.421	0.172	64	9.02	9.77	9.448	0.192
Pa-M3	87	6.65	7.35	7.008	0.167	47	6.68	7.35	7.026	0.174	40	6.65	7.28	7.052	0.16	64	6.65	7.35	7.02	0.168
MI-M3	87	5.43	6.02	5.74	0.141	47	5.45	6.02	5.719	0.136	40	5.43	6	5.764	0.145	64	5.43	5.95	5.719	0.127
C-P4	87	3.57	4.13	3.815	0.119	47	3.62	4.13	3.83	0.126	40	3.57	4	3.797	0.107	64	3.57	4.13	3.825	0.125
P2-P4	87	2.37	2.95	2.698	0.116	47	2.43	2.95	2.709	0.113	40	2.37	2.95	2.67	0.117	64	2.37	2.95	2.701	0.121

Spin		Switzerland					Moravia					Slovakia					
	n	Mean	n	mean	max	Mean	SD	n	mean	max	Mean	SD	n	mean	max	Mean	SD
LCc	1	26.15	15	20.7	22.07	21.166	0.356	17	30.52	22	21.304	0.442	66	20.44	22.42	21.385	0.455
LCb	1	19.22	12	19.75	20.42	20.028	0.2	16	19.52	20.85	20.184	0.421	84	19.55	21.78	20.307	0.423
LaZ	1	14.16	11	13.28	13.92	13.623	0.173	16	13.25	14.15	13.78	0.307	64	12.88	14.22	13.615	0.306
Lai	1	5.27	16	4.88	5.55	5.109	0.172	17	4.68	5.5	5.103	0.221	66	4.65	5.62	5.118	0.181
LaInf	1	5.34	16	5.07	5.75	5.374	0.186	17	5.05	6.05	5.424	0.245	66	4.93	6	5.423	0.218
LaN	1	9.64	15	9.21	10	9.602	0.203	17	9.88	10.02	9.914	0.289	66	9.07	10.08	9.614	0.199
LaS	1	18.1	14	9.72	10.37	10.169	0.187	17	9.72	10.52	10.124	0.216	64	9.25	10.57	9.974	0.251
VN	1	7.5	12	7.27	8	7.545	0.256	16	7.15	7.9	7.528	0.205	85	7.05	8	7.522	0.211
VN2	1	9.85	12	8.8	9.5	9.116	0.266	12	8.68	9.92	9.308	0.325	66	8.4	9.5	9	0.25
M-M3	1	9.72	16	9.93	10.89	10.389	0.219	16	9.73	10.67	10.255	0.231	66	9.95	11	10.345	0.209
C-M3	1	8.27	16	8.13	9.27	8.73	0.257	15	8.35	9.05	8.749	0.245	85	8.42	9.17	8.818	0.202
P4-M3	1	6.12	16	5.4	7.05	6.204	0.335	12	6.08	6.83	6.352	0.39	66	6.23	6.72	6.376	0.13
M4-M3	1	5.07	16	4.81	5.67	5.086	0.229	17	4.73	5.42	5.109	0.172	66	4.9	5.65	5.287	0.113
C-P4	1	3.85	16	3.6	4.77	3.996	0.267	15	3.6	4.7	3.983	0.187	85	3.43	4.67	3.945	0.203
P2-P3	1	1.15	16	1.09	1.54	1.211	0.108	17	1.04	1.31	1.169	0.067	64	1.04	1.41	1.289	0.068
C-C	1	5.67	16	5.33	5.88	5.579	0.158	12	5.15	5.83	5.633	0.187	85	5.33	6.22	5.784	0.164
P4-P4	1	7.22	15	6.65	7.1	6.908	0.153	16	6.88	7.2	6.971	0.206	66	6.65	7.3	7.006	0.146
M3-M3	1	9.02	15	8.25	9.25	8.778	0.257	17	8.57	9.92	8.85	0.388	66	8.35	9.45	8.88	0.25
L-Md	1	15.87	16	13.43	16.66	15.938	0.295	16	15.52	16.9	16.217	0.366	87	15.92	17.72	16.285	0.425
C-E	1	4.9	16	4.85	5.32	5.066	0.157	16	4.67	5.48	5.273	0.203	64	4.75	6.02	5.19	0.199
T3-M3	1	10.3	16	10.1	11.62	10.769	0.333	16	10.37	11.3	10.762	0.291	65	10.3	11.4	10.867	0.224
C-M3	1	8.93	16	8.22	10.2	9.35	0.415	16	8.08	9.85	9.419	0.213	86	8.6	10.2	9.477	0.238
P4-M3	1	6.87	16	5.67	7.87	6.926	0.455	16	6.7	7.4	6.928	0.201	87	6.6	7.6	7.005	0.178
M4-M3	1	5.75	16	5.25	6.55	5.638	0.3	16	5.37	6.13	5.671	0.174	87	5.4	6	5.712	0.125
C-P4	1	3.55	16	3.57	5	3.961	0.307	18	3.52	4.08	3.801	0.152	84	3.55	4.25	3.887	0.135
P2-P4	1	2.37	16	2.55	3	2.751	0.11	18	2.45	2.93	2.731	0.121	85	2.49	3.15	2.738	0.137

	Bulgaria					Albania					Romania					W. Turkey				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	36	20.35	22.1	21.371	0.453	7	20.47	22.35	21.213	0.608	4	20.35	21.35	21.045	0.467	5	20.17	21.06	20.696	0.395
LCh	34	19.15	21	20.26	0.442	6	19.53	20.87	20.03	0.325	3	19.15	20.2	19.817	0.58	5	18.82	20.17	19.46	0.547
La2	26	12.87	14.19	13.646	0.331	6	12.95	14.08	13.46	0.465	2	12.38	13.81	13.595	0.304	5	13.1	13.73	13.49	0.263
La3	39	4.75	5.42	5.045	0.16	7	4.72	5.22	4.949	0.166	4	4.75	5.1	4.896	0.152	5	5.02	5.32	5.172	0.166
LaInI	40	4.95	5.62	5.465	0.183	7	5.13	5.9	5.39	0.266	4	4.95	5.5	5.333	0.259	5	5.1	5.62	5.365	0.222
LaIn	37	9.21	10.22	9.596	0.202	7	9.2	9.93	9.456	0.271	4	9.42	9.5	9.48	0.04	5	9.13	9.82	9.554	0.277
LaInI	37	9.27	10.24	9.798	0.229	7	9.27	9.9	9.481	0.249	4	9.27	10	9.64	0.321	5	9.23	10.25	9.95	0.192
VN	33	7.13	8.05	7.58	0.24	6	7.1	8.07	7.342	0.367	3	7.3	7.58	7.42	0.144	5	7.13	7.73	7.506	0.274
VN2	28	8.6	9.83	9.075	0.286	4	8.7	9.46	8.96	0.334	4	8.65	9.02	8.873	0.157	4	8.48	9.18	8.895	0.333
I1-M3I	42	9.72	10.8	10.324	0.264	7	10	10.98	10.307	0.319	4	9.82	10.48	10.18	0.286	5	9.62	10.47	10.146	0.325
C-M3I	42	8.06	9.12	8.734	0.258	7	8.42	9.25	8.769	0.264	4	8.27	8.9	8.65	0.281	5	8.22	8.82	8.615	0.239
P4-M3I	42	5.87	6.6	6.332	0.137	7	6.07	6.58	6.3	0.193	4	6.05	6.35	6.25	0.136	5	6.09	6.4	6.224	0.154
M1-M3I	42	4.74	5.4	5.115	0.148	7	5.05	5.4	5.169	0.14	4	4.87	5.17	5.038	0.129	5	5.02	5.28	5.134	0.116
C-P4I	42	3.65	4.32	3.948	0.176	7	3.52	4.15	3.903	0.193	4	3.7	4.05	3.888	0.179	5	3.57	3.92	3.834	0.146
P2-P3I	42	1.05	1.39	1.204	0.089	7	1.09	1.33	1.219	0.092	4	1.06	1.24	1.173	0.081	5	1.03	1.33	1.262	0.111
C-C	41	4.85	6.03	5.643	0.241	7	5.32	5.95	5.563	0.246	4	4.85	5.82	5.413	0.411	5	5.23	6.02	5.796	0.262
P4-P4I	41	6.28	7.35	6.945	0.261	7	6.5	7.12	6.8	0.247	4	6.6	6.95	6.838	0.168	5	6.75	7.25	6.972	0.213
M3-M3I	40	7.34	9.32	8.362	0.352	7	8.28	9.27	8.439	0.332	4	7.34	8.9	8.43	0.617	5	8.48	8.82	8.652	0.143
LMd	43	15.25	17.15	16.183	0.403	7	15.42	16.85	15.99	0.497	4	15.25	16.25	15.863	0.433	5	15.48	16.08	15.794	0.249
CrH	40	4.53	5.92	5.128	0.274	7	4.53	5.32	4.919	0.236	4	4.53	5.21	4.885	0.318	5	5.03	5.23	5.116	0.092
I1-M3I	43	10.27	12.47	10.927	0.231	7	10.5	11.4	10.931	0.295	4	10.6	11.16	10.865	0.229	5	10.68	10.97	10.808	0.122
C-M3I	43	8.85	9.85	9.47	0.317	7	9.11	9.93	9.479	0.253	4	9.15	9.68	9.403	0.245	5	9.27	9.48	9.404	0.181
P4-M3I	43	6.5	7.42	7.02	0.206	7	6.93	7.4	7.074	0.173	4	6.72	7.25	6.995	0.233	5	6.78	7.1	6.92	0.118
M1-M3I	43	5.27	5.95	5.703	0.132	7	5.62	6.05	5.779	0.152	4	5.55	5.9	5.698	0.15	5	5.55	5.72	5.644	0.068
C-P4I	43	3.6	4.23	3.886	0.143	7	3.58	4.2	3.881	0.207	4	3.6	3.87	3.773	0.119	5	3.8	4.22	3.993	0.166
P2-P4I	43	2.52	3.55	2.791	0.17	7	2.32	2.85	2.749	0.184	4	2.68	2.95	2.8	0.131	5	2.55	2.87	2.728	0.12

	E Turkey					Transcaucasia					N Iran					Turkmenistan				
	n	mean	std	Mean	SD	n	mean	std	Mean	SD	n	mean	std	Mean	SD	n	mean	std	Mean	SD
LCr	17	21.27	22.6	22.939	0.384	15	21.68	22.75	22.161	0.351	3	22.1	22.32	22.197	0.112	20	20.7	22.75	21.452	0.584
LCh	13	20.27	21.78	21.051	0.458	12	20.58	21.78	21.088	0.394	3	21.02	21.33	21.123	0.179	20	19.53	21.35	20.485	0.566
LaZ	17	13.87	14.82	14.149	0.322	17	13.55	14.7	14.115	0.284	2	13.72	14.07	13.895	0.147	13	12.85	14.15	13.472	0.383
LaI	18	4.9	5.67	5.236	0.388	16	4.95	5.37	5.283	0.112	1	5.1	5.39	5.264	0.194	19	4.63	5.32	5.629	0.151
Labuf	18	5.18	6.38	5.766	0.255	16	5.45	6.22	5.811	0.23	4	5.55	5.88	5.738	0.164	20	5.41	5.94	5.613	0.176
LaN	14	8.97	10.4	9.754	0.188	16	9.03	10.42	9.794	0.116	4	9.32	10.05	9.775	0.119	20	9	9.85	9.488	0.231
LaM	13	9.55	10.47	10.267	0.237	16	9.27	10.75	10.198	0.38	1			9.95		20	9.32	10.2	9.789	0.237
VN	13	7.22	8.02	7.618	0.261	16	7.02	8.23	7.726	0.284	4	7.33	7.7	7.483	0.179	20	6.8	7.95	7.571	0.173
VN2	12	8.92	9.52	9.283	0.194	2	8.55	9.63	9.231	0.306	0					16	8.1	9.42	8.788	0.307
DI/MSI	15	9.62	11.23	10.785	0.437	18	8.7	11.22	10.734	0.614	5	9.97	10.78	10.548	0.327	20	10.25	11.23	10.654	0.261
C/MSI	17	9.05	9.57	9.809	0.368	18	7.4	9.55	9.187	0.47	6	8.42	9.19	9.037	0.119	20	8.63	9.32	9.768	0.236
PM/MSI	17	5.1	6.1	6.458	0.209	18	5.5	6.87	6.588	0.304	6	6.22	6.58	6.45	0.128	20	6.32	6.85	6.531	0.185
MI/MSI	16	4.75	5.52	5.14	0.213	18	4.48	5.85	5.329	0.29	6	4.77	5.43	5.227	0.141	20	5	5.62	5.383	0.168
C/P4	13	3.6	4.45	4.091	0.235	18	3.47	5.48	4.198	0.401	6	3.92	4.37	4.063	0.147	20	3.42	4.28	3.981	0.207
P2/P3	12	1.11	1.41	1.274	0.099	18	1.09	1.46	1.291	0.097	6	1.13	1.43	1.283	0.113	20	0.96	1.39	1.218	0.115
C-C	11	4.93	6.3	5.76	0.352	14	5.55	6.18	5.878	0.216	4	5.58	6.32	5.87	0.134	20	5.25	6.15	5.69	0.234
PM/P4	16	6.5	7.7	7.179	0.283	15	6.73	7.62	7.291	0.23	4	6.63	7.45	7.053	0.368	20	6.58	7.72	7.016	0.269
MDV/MDV	16	8	9.55	9.839	0.327	15	8.6	9.55	9.133	0.226	4	8.67	9.27	9.46	0.278	20	8.2	9.58	8.813	0.352
LMd	18	16.47	17.27	16.983	0.241	17	15.9	17.5	16.966	0.457	6	16.02	17.02	16.693	0.301	20	15.67	17.3	16.442	0.457
C/HI	17	4.9	5.75	5.451	0.19	17	4.65	5.87	5.488	0.297	6	4.82	5.48	5.12	0.244	20	4.65	5.42	5.055	0.232
I/I/MSI	12	10.65	11.02	11.259	0.287	18	9.9	11.78	11.382	0.452	6	10.8	11.45	11.25	0.239	20	11	11.75	11.383	0.236
C/MSI	13	9.22	10.27	9.847	0.294	18	8.9	10.27	9.948	0.321	5	9.7	9.95	9.866	0.101	20	9.53	10.32	9.886	0.224
PM/MSI	13	6.87	7.62	7.162	0.225	18	7.1	7.72	7.414	0.172	6	6.9	7.55	7.255	0.232	20	7.23	7.87	7.415	0.134
MI/MSI	14	5.68	6.25	5.87	0.183	18	5.72	6.28	6.008	0.152	6	5.67	6.05	5.853	0.147	20	5.71	6.11	5.98	0.155
C/P4	13	3.75	4.37	4.067	0.169	18	3.47	4.33	4.117	0.214	5	3.95	4.22	4.08	0.107	20	3.7	4.32	4.018	0.168
P2/P4	13	2.33	3.22	2.868	0.231	18	2.57	3.08	2.889	0.15	1	2.67	2.95	2.78	0.098	20	2.62	3.1	2.855	0.117

		Uzbekistan					N Kyrgyzstan				
		n	mean	std	Mean	SD	n	mean	std	Mean	SD
LCr	8	21.88	21.95	21.383	0.113	15	20.43	21.85	21.238	0.367	
LCh	8	19.98	20.82	20.177	0.318	15	13.47	20.62	20.227	0.337	
LaZ	6	13.23	14.57	13.638	0.414	12	14.13	18.781	0.331		
LaI	6	4.92	5.27	5.112	0.155	15	4.8	5.42	5.117	0.171	
Labuf	6	5.52	5.95	5.735	0.158	15	5.58	6.07	5.815	0.162	
LaN	8	9.48	10	9.747	0.205	15	9.32	10.07	9.688	0.217	
LaM	8	9.15	10.47	10	0.285	15	9.15	10.41	10.134	0.195	
VN	8	7.32	7.8	7.532	0.213	15	7.32	7.78	7.589	0.127	
VN2	8	8.63	9.28	8.952	0.274	11	8.67	9.39	9.054	0.184	
DI/MSI	8	10.32	10.94	10.527	0.223	15	9.85	10.88	10.358	0.241	
C/MSI	8	6.53	9.27	8.188	0.248	15	8.33	9.17	8.689	0.214	
PM/MSI	8	6.25	6.7	6.415	0.177	15	6.1	6.72	6.387	0.163	
MI/MSI	8	5.1	5.45	5.297	0.12	15	4.77	5.49	5.252	0.173	
C/P4	8	3.07	4.28	4.002	0.309	15	3.7	4.02	3.875	0.096	
P2/P3	8	1.19	1.46	1.31	0.093	15	1.06	1.33	1.199	0.058	
C-C	8	5.78	6.12	5.96	0.137	15	5.58	6.07	5.886	0.13	
PM/P4	8	7.02	7.63	7.21	0.213	15	6.77	7.53	7.245	0.251	
MDV/MSI	8	8.65	9.35	8.943	0.283	15	8.66	9.98	9.123	0.308	
LMd	8	15.85	16.86	16.29	0.352	15	15.27	16.82	16.063	0.364	
C/HI	8	4.87	5.4	5.1	0.221	15	4.83	5.37	5.108	0.135	
I/I/MSI	8	16.84	17.4	17.095	0.209	15	10.5	11.29	10.893	0.225	
C/MSI	8	9.33	10.92	9.762	0.544	15	9.03	9.88	9.497	0.217	
PM/MSI	8	6.8	7.36	7.181	0.228	15	6.71	7.32	7.031	0.152	
MI/MSI	8	5.57	5.8	5.762	0.11	15	5.23	5.91	5.719	0.178	
C/P4	8	3.82	4.12	3.943	0.12	15	3.6	4.12	3.867	0.158	
P2/P4	8	2.71	3.05	2.883	0.124	14	2.5	2.85	2.676	0.117	

*Myotis nattereri*

	N-Africa					Spain					Bohemia					Moravia				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LCr	19	14.9	15.85	15.242	0.262	4	15.2	16	15.625	0.311	20	14.68	16.45	15.655	0.397	12	15.6	16.35	15.878	0.193
LCb	19	13.8	14.98	14.235	0.249	4	14	14.85	14.483	0.329	26	13.25	15.27	14.467	0.386	11	14.08	15.04	14.732	0.235
LaZ	19	5.15	9.32	5.479	0.168	3	9.45	9.72	9.623	0.15	32	5.1	10.7	9.769	0.364	13	9.72	10.43	10.064	0.203
LaI	19	3.4	3.72	3.589	0.093	4	3.3	3.85	3.563	0.195	26	3.67	4.45	3.962	0.152	15	3.75	4.1	3.889	0.107
LaIaI	19	3.6	3.95	3.782	0.101	5	3.8	4	3.912	0.094	37	3.52	4.7	3.95	0.139	16	3.7	4.16	3.948	0.128
LaN	19	7.37	7.97	7.683	0.195	6	7.34	7.82	7.62	0.204	30	7.6	8.38	7.896	0.16	14	7.5	8.17	7.991	0.173
LaM	19	7.48	7.85	7.66	0.118	5	7.43	7.75	7.612	0.138	32	3.07	8.38	7.743	0.205	11	7.65	8.17	7.992	0.15
VN	19	5.45	6.78	5.766	0.274	5	5.47	5.5	5.49	0.014	35	5.2	5.83	5.59	0.157	12	5.5	5.9	5.708	0.158
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1U-MC1	16	6.31	7.15	6.894	0.181	5	7.17	7.5	7.318	0.119	19	6.8	7.9	7.287	0.246	15	7.12	7.65	7.383	0.161
C-MC1	19	3.55	5.91	5.727	0.101	6	3.9	6.17	6.05	0.095	40	5.62	6.5	6.184	0.182	15	5.9	6.32	6.145	0.13
P4-MC1	19	4.11	4.4	4.237	0.08	1			4.4		40	4	4.6	4.381	0.136	15	4.21	4.57	4.404	0.103
M1-MC1	19	3.32	3.58	3.462	0.059	1	3.55	3.51	3.422	0.064	40	3.23	3.85	3.543	0.115	15	3.48	3.7	3.597	0.053
M1-MC2	1			2.82		1			3.9		40	2.6	3	2.791	0.087	15	2.71	2.95	2.823	0.065
C-C	19	3.72	4.05	3.872	0.101	5	4	4.33	4.1	0.135	39	3.52	4.42	4.025	0.165	13	3.82	4.3	4.015	0.106
P4-P4	19	4.46	5.12	4.842	0.114	5	5	5.33	5.134	0.136	38	4.85	5.51	5.171	0.168	15	5.1	5.45	5.277	0.123
M3-MC1	19	5.8	6.38	6.14	0.255	5	6.85	6.75	6.8	0.06	39	5.92	7	6.454	0.216	15	6.42	6.9	6.613	0.139
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1-M4	19	10.6	11.7	10.996	0.272	6	11.35	11.5	11.368	0.132	20	10.4	12.25	11.464	0.261	16	11.35	11.95	11.63	0.106
C-M4	18	3	3.58	3.296	0.118	0			3		3	3.4	3.2	3.283	0	11	3.23	3.5	3.352	0.079
1U-MC2	19	7.16	7.61	7.489	0.12	5	7.54	8	7.794	0.173	39	7.1	8.1	7.743	0.235	15	7.7	8.2	7.907	0.171
C-MC2	19	5.88	6.55	6.129	0.113	6	6.3	6.78	6.437	0.131	39	6	6.84	6.455	0.185	15	6.37	6.8	6.578	0.14
P4-MC2	19	4.23	4.57	4.461	0.089	5	4.57	4.83	4.704	0.097	38	4.45	4.95	4.705	0.113	15	4.65	4.9	4.853	0.079
M1-MC2	19	3.66	3.86	3.727	0.06	5	3.63	4	3.872	0.071	40	3.67	4.12	3.846	0.11	15	3.8	4.1	3.944	0.082
C-P4	18	2.3	2.59	2.415	0.069	0			0		0			0		0			0	
C-MC1	1			3.8		1			3.84		40	3.55	4.2	3.865	0.142	15	3.75	4.1	3.922	0.111
P4-MC1	1			2.89		1			2.87		40	1.99	2.23	2.128	0.055	15	2.1	2.3	2.151	0.062
M1-MC2	1			2.61		1			2.62		40	2.43	2.8	2.613	0.073	15	2.35	2.78	2.672	0.064
P4a	19	0.63	0.84	0.735	0.044	1			0.8		39	0.77	0.96	0.853	0.039	15	0.77	0.92	0.852	0.044
P4b	1	0.6	0.68	0.643	0.036	1			0.63		39	0.6	0.75	0.656	0.038	15	0.6	0.7	0.631	0.03
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Poland					Slovakia					Bulgaria					Greece					
n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	
LCr	14	13.38	16.5	15.926	0.315	12	13.1	15.99	15.482	0.268	30	15.3	16.35	15.634	0.274	18	15.2	16.38	15.801	0.307
LCb	14	14.45	15.67	14.846	0.314	11	14.2	15.04	14.611	0.248	20	14.23	15.15	14.579	0.256	18	14.25	15.09	14.732	0.226
LaZ	8	9.65	10.78	10.137	0.221	8	9.3	10.15	9.719	0.248	22	9.55	10.4	9.862	0.248	16	9.24	10.5	10.079	0.225
LaI	16	5.8	6.5	6.013	0.134	11	5.65	6.05	5.821	0.124	20	5.55	5.95	5.743	0.098	18	5.65	6.13	5.854	0.14
LaIaI	16	3.9	4.2	4.078	0.087	12	3.5	4.05	3.858	0.173	20	3.65	4.3	3.913	0.125	18	3.92	4.28	4.054	0.097
LaN	14	7.85	8.38	8.048	0.172	12	7.65	8.1	7.884	0.119	20	7.59	8.35	7.853	0.174	18	7.23	8.18	7.816	0.225
LaM	15	7.7	8.32	8.017	0.172	11	7.58	8	7.852	0.109	20	7.4	8.15	7.797	0.197	18	7.48	8.08	7.866	0.104
VN	16	5.7	6.3	5.897	0.168	12	5.43	6.15	5.77	0.196	20	5.35	6.15	5.7	0.2	18	5.36	5.79	5.567	0.135
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1U-MC1	16	6.95	7.68	7.199	0.198	11	7	7.83	7.363	0.226	19	6.97	7.73	7.336	0.196	18	7.15	7.65	7.464	0.124
C-MC1	16	5.82	6.49	6.187	0.149	12	5.8	6.32	6.044	0.145	19	5.89	6.42	6.077	0.159	18	6.01	6.4	6.239	0.109
P4-MC1	16	4.19	4.7	4.374	0.123	12	4.18	4.53	4.358	0.098	19	4.15	4.7	4.381	0.143	18	4.24	4.62	4.463	0.073
M1-MC1	16	3.34	3.66	3.507	0.101	12	3.38	3.66	3.547	0.088	19	3.37	3.8	3.584	0.13	18	3.34	3.77	3.626	0.067
M1-MC2	1			2.8		12	3.6	2.92	2.772	0.134	19	2.5	3	2.834	0.175	18	2.78	2.98	2.864	0.055
C-C	15	3.92	4.31	4.059	0.106	12	3.9	4.32	4.068	0.104	18	3.91	4.2	4.046	0.101	18	3.9	4.3	4.099	0.107
P4-P4	16	5.1	5.5	5.248	0.181	12	4.95	5.7	5.261	0.189	19	5.03	5.25	5.126	0.097	18	5.14	5.53	5.301	0.102
M3-MC1	16	6.28	6.72	6.51	0.144	12	6.3	6.85	6.534	0.195	19	6.22	6.82	6.496	0.186	18	6.42	6.8	6.457	0.214
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1-M4	14	10.81	11.78	11.384	0.351	12	10.75	11.65	11.316	0.272	20	11.97	11.91	11.368	0.254	18	11.35	12	11.498	0.023
C-M4	0					10	3.02	3.45	3.282	0.134	18	3	3.6	3.333	0.162	0				
1U-MC2	14	7.53	8.3	7.814	0.216	12	7.4	8.1	7.754	0.217	18	7.42	8.2	7.783	0.208	18	7.9	8.1	7.963	0.048
C-MC2	14	6.16	6.55	6.366	0.203	12	6.2	6.75	6.447	0.16	19	6.11	6.87	6.494	0.165	18	6.05	6.76	6.553	0.129
P4-MC2	14	4.49	5.08	4.732	0.144	12	4.4	4.82	4.683	0.128	19	4.43	5	4.728	0.14	18	4.64	4.91	4.779	0.075
M1-MC2	14	3.75	4.18	3.964	0.122	12	3.6	4.02	3.848	0.12	19	3.63	4.17	3.907	0.132	18	3.77	4.07	3.928	0.072
C-P4	0					0			0		0			0		0				
C-MC1	0					12	3.7	4.11	3.878	0.116	19	3.64	4.06	3.871	0.107	18	3.74	4.11	3.938	0.091
P4-MC1	14	3.02	3.29	3.139	0.045	12	2	2.15	2.096	0.081	19	2	2.25	2.132	0.071	18	2.1	2.22	2.119	0.041
M1-MC2	12	2.56	2.83	2.642	0.044	12	2.43	2.73	2.626	0.083	19	2.5	2.8	2.644	0.072	18	2.5	2.7	2.628	0.055
P4a	14	0.77	0.93	0.844	0.019	12	0.68	0.9	0.81	0.07	19	0.78	0.94	0.869	0.051	18	0.82	0.91	0.876	0.023
P4b	14	0.59	0.69	0.64	0.03	12	0.6	0.71	0.652	0.042	19	0.62	0.92	0.685	0.069	18	0.6	0.72	0.674	0.026

	W-Turkey					Kurdistan					Transcaucasia					Turkmenistan				
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LC+	28	15.4	16.13	15.854	0.184	8	15.73	16.63	16.344	0.347	7	15.7	16.2	15.976	0.203	5	16.1	16.3	16.2	0.071
LC+	17	14.4	15.25	14.756	0.22	7	15.09	15.46	15.263	0.187	8	14.75	15.22	15.04	0.184	5	14.97	15.3	15.11	0.143
LaZ	15	9.0	10.79	9.853	0.487	8	9.45	10.45	10.23	0.164	1			10.1		3	9.6	10	9.867	0.115
LaI	28	3.33	4	3.668	0.102	8	3.38	3.95	3.699	0.122	7	3.47	4	3.663	0.171	5	3.7	3.7	3.7	0
Latel	28	3.7	4.06	3.962	0.097	0					5	3.83	4.05	3.976	0.084	1			3.95	
LaN	28	7.4	8.05	7.748	0.195	0					5	7.63	8.2	7.9	0.233	5	7.77	8	7.874	0.092
LaM	28	7.6	8.12	7.854	0.167	0					5	7.73	7.95	7.86	0.003	1			7.83	
VN	28	4.92	5.79	5.548	0.192	0					5	5.4	5.8	5.596	0.183	1			5.56	
IR-MO	28	7.21	7.63	7.411	0.149	0					4	7.63	7.82	7.716	0.085	1			7.7	
C-MO	28	6	6.37	6.142	0.126	8	6.12	6.43	6.313	0.108	5	6.3	6.5	6.39	0.096	5	6.4	6.6	6.484	0.079
PA-MO	28	4.33	4.54	4.439	0.099	0					4	4.47	4.6	4.54	0.054	1			4.5	
MI-MO	28	3.34	3.7	3.531	0.089	8	3.31	3.73	3.524	0.081	4	3.7	3.78	3.75	0.034	1			3.7	
MI-MO	8	3.74	3.96	3.844	0.073	0					4	2.9	2.95	2.93	0.024	1			2.91	
C-C	28	3.93	4.25	4.073	0.095	0					4	3.98	4.2	4.125	0.104	1			3.93	
PA-PH	28	5	5.34	5.159	0.102	0					4	5.13	5.46	5.385	0.117	1			5.18	
MI-MO	28	5.16	6.07	5.591	0.197	0					4	6.42	6.87	6.553	0.213	1			6.48	
LMO	28	11.25	11.8	11.489	0.175	8	10.76	11.3	11.065	0.209	8	11.6	12.1	11.755	0.209	5	11.7	11.9	11.8	0.071
COI	23	3.1	3.7	3.453	0.196	8	3.44	3.8	3.556	0.122	0					0				
IR-MO	27	7.17	8.1	7.718	0.248	0					4	8	8.35	8.179	0.155	1			8	
C-MO	28	6.16	6.72	6.476	0.145	4	6.66	6.83	6.769	0.074	0					4	6.6	6.94	6.772	0.114
PA-MO	28	4.56	4.9	4.729	0.099	8	4.64	5.02	4.834	0.059	4	4.9	5.01	4.963	0.050	1			4.9	
MI-MO	28	3.75	4	3.863	0.086	8	3.94	4.15	4.059	0.07	4	3.99	4.12	4.053	0.056	1			4.07	
C-PH	0					0					0					0				
C-MO	8	3.85	4.08	3.963	0.073	0					4	4	4.18	4.09	0.074	1			4	
PA-MO	8	2.05	2.27	2.191	0.085	0					4	2.22	2.27	2.233	0.041	1			2.2	
MI-MO	8	2.6	2.72	2.672	0.046	0					4	2.7	2.82	2.773	0.053	1			2.76	
PA-MO	8	0.81	0.82	0.86	0.023	8	0.92	1	0.959	0.031	4	0.8	0.96	0.895	0.074	1			0.87	
PA-MO	8	0.56	0.72	0.631	0.053	8	0.7	0.81	0.755	0.042	4	0.7	0.72	0.713	0.01	1			0.63	
	Israel					N-Iran														
	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD	n	min	max	Mean	SD
LC+	4	17.23	18.29	17.919	0.4	5	16.8	17.3	17.23	0.311										
LC+	8	14.05	15.7	14.799	0.38	5	15.8	16.3	16.18	0.259										
LaZ	5	9.3	10.37	10.092	0.279	3	10.3	10.6	10.7	0.146										
LaI	8	3.38	3.9	3.754	0.403	2	4	4.4	4.14	0.195										
Latel	7	3.72	4.18	3.96	0.136	1			4.6											
LaN	8	7.73	8.1	7.929	0.131	5	8.95	9	8.62	0.244										
LaM	7	7.4	8.13	7.933	0.199	1			8.3											
VN	7	5.3	6.1	5.83	0.183	1			6.4											
IR-MO	7	7.12	7.57	7.394	0.148	2			8.2											
C-MO	8	6.88	8.22	7.672	0.151	5	6.6	6.93	6.764	0.159										
PA-MO	7	4.35	4.5	4.396	0.131	1			5.85											
MI-MO	7	3.45	3.67	3.553	0.08	1			4.81											
MI-MO	5	2.98	3.87	3.314	0.034	1			3.14											
C-C	7	4	4.23	4.082	0.128	1			4.7											
PA-PH	7	3.16	3.33	3.15	0.078	1			3											
MI-MO	7	6	6.5	6.338	0.174	1			7.25											
LMO	8	11.85	12	11.984	0.32	3	12.3	12.9	12.614	0.343										
COI	2	3.2	3.4	3.3	0.141	0														
IR-MO	3	7.5	8	7.817	0.185	1			8.7											
C-MO	5	6.25	6.71	6.545	0.186	5	6.8	7.3	7.16	0.167										
PA-MO	7	4.54	4.8	4.699	0.102	1			5.33											
MI-MO	7	3.71	3.91	3.807	0.073	1			4.38											
C-PH	0					0														
C-MO	5	3.41	4.15	4.012	0.123	1			4.37											
PA-MO	5	2.13	2.25	2.19	0.054	1			2.4											
MI-MO	5	2.6	2.9	2.643	0.057	1			2.9											
PA-MO	5	0.84	1.13	0.954	0.113	0														
PA-MO	5	0.64	0.72	0.678	0.033	0														

**Odour-based discrimination among populations of Striped field mice  
(*Apodemus agrarius*)**

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Received October 20, 1993; Accepted February 9, 1995

Published June 22, 1995

**Behavioural preference, choice test, *Apodemus agrarius***

**Abstract.** Mice coming from populations of different geographical origin (Europe: Bohemia, Slovenia; Asia: Russian Far East) served as subjects. Simple choice tests were carried out in order to test behavioural discrimination among individual populations. Animals of all populations under study spent more time in the vicinity of conspecific odours of animals from another population. This preference was more apparent for odours of animals from related populations. European mice significantly preferred another European over Far East populations. No tendency to seek odours of unfamiliar animals from subject's own population was found.

**INTRODUCTION**

During the last decade extraordinary abilities of rodent olfaction as kin (Dewsbury 1988, Porter 1988, Waldman 1988, Barnard et al. 1991), the genotype (Beauchamp et al. 1988, Lenington et al. 1988, Manning et al. 1992) and individual (Wolton 1984) recognition (and discrimination) were discovered. Our opinion is, that in this new context a reevaluation of the other phenomena dealing with odour-based recognition or discrimination between more and less related animals is necessary. Odour-based discrimination between species is a well-known phenomenon (Moore 1965, Smith 1965, Doty 1972, Sokolov et al. 1984, 1990, Sokolov & Kotenkova 1987, Kotenkova et al. 1989, Dempster & Perrin 1990, Frynta et al. 1992, etc.), to which most attention was devoted in the 1960s as a result of interest in speciation. Taking into account cases of discrimination among individual populations of single species (Cox 1984, 1989) we can conclude that a wide range of discrimination processes based on olfaction has been described in rodents. Discrimination processes operating on an upper level, i.e., population and species, could be evaluated simply as an extension of those ones operating on lower levels (genotype, kinship, individual) and vice versa. It cannot be excluded that the same proximate mechanism is responsible for all these phenomena in rodents. Also the ultimate causes of these abilities to discriminate between more and less related (or familiar) odours may be attributed to a single complex of factors. It is of interest in this context that discrimination on each level includes both mating preferences and regulation of social relationships. It has to be remarked here that in social anthropology a single principle of kinship, i.e., distinction between more and less related individuals or social groups, has been repeatedly found to determine structure of social interactions irrespective to their hierarchical level. The classical description of such a phenomenon in Nuer society by Evans-Pritchard (1979) is still highly stimulating.

Above mentioned hypothesis emphasizing possible continuity between discrimination processes operating on different levels cannot be evaluated without a detailed description of all these phenomena. Unfortunately, only relatively scarce experimental data are available especially in



the case of discrimination between conspecific populations.

This study is an attempt to test odour-based discrimination among different populations of conspecifics in striped-field mice (*Apodemus agrarius*) using simple behavioural methods. This species was selected because of its large range and unusual evolutionary history. We decided to use animals coming from three populations of different degree of relatedness and geographical origin: from Bohemia, Slovenia, and the Russian Far East. The former two populations (both European) are related to each other, while the later one is apparently distant.

The present range of *Apodemus agrarius*, extending from Southern China through Manchuria, Korea, Russian Far East, Southern Siberia, Kazakhstan up to Central Europe, is extremely large (Corbet 1978, Karaseva et al. 1992). However, despite of its wide distribution in Europe, this species seems to be late (Early Holocene) immigrant from Asia (Böhme 1978). Therefore, different European populations ought to be closely related to each other. This assumption was supported by most authors (Bobrinskij et al. 1965, Černucha et al. 1986). The majority of European populations are supposed belong to a single subspecies, *Apodemus agrarius agrarius* (Pallas, 1778). The only exceptions are two isolates in the Balkan Peninsula: *A. a. kahmanni* Malec & Storch, 1963 and *A. a. istriani* Kryštufek, 1985 (Kryštufek 1985, Vohralík & Sofianidou 1992).

All the animals from European populations used in our experiments belonged to subspecies *A. a. agrarius*. In spite of the fact that the geographical distance between Bohemia and Slovenia is not so great, these regions were probably colonized by *Apodemus agrarius* using different migration routes (northern route for the former and southern for the later territory). These routes are separated by the Carpathians and by large areas without any presence of this species in Central Bohemia and Moravia (Kratochvíl et al. 1976).

Due to Asian origin of this species much greater differentiation among individual populations should be expected in Asian part of its range. Unfortunately, taxonomy and relationships of different Asian populations of this species in Russia, Korea and China are still unclear. Immunological data (Černucha et al. 1986) revealed considerable differentiation even among different populations from Asian parts of Russian territory (regions: Altaj, Chabarovsk, Primor'e). Animals from Russian Far East in our experiments belonged to the subspecies *A. a. ningpoensis* (Swinhoe, 1870) - synonymum: *A. a. manchuricus* Thomas, 1898 (cf. Vinogradov & Gromov 1952, Corbet 1978, Kostenko 1984).

## MATERIAL AND METHODS

**Subjects.** Adult, socially experienced *Apodemus agrarius* from following four geographical regions were studied.

1) Bohemia (Czech Republic) Four individuals (2 males and 2 females) captured near the village Rybníček in April 1992, fifteen individuals (8 males and 7 females) captured in the village Chýbčská in October 1992. Both localities are situated in Northern Bohemia (district Děčín) about 15 km apart.

2) Slovenia. Sava River valley near the town Brežice (Eastern Slovenia). Five individuals (3 males and 2 females) captured in July 1992, ten animals (5 males and 5 females) captured in August 1992; five individuals (4 males and 1 female) born in laboratory in late August 1992.

3) Turkey. One female captured near the village Igneada (district Edirne) in May 1992.

4) Far East. Twelve individuals (5 males and 7 females) of the first and second generation born in laboratory. Two pairs of ancestral animals were captured in the vicinity of the town Vjazemskij (district Chabarovsk) in Russian Far East in September 1990.

In addition (in experiment 1), two pairs of laboratory-born *Apodemus peninsulae* (Thomas, 1906) from colony originating in Russian Far East were used as odour source.

**Housing conditions.** All animals were kept under an artificial 12 L : 12 D light cycle and housed by pairs in plastic cages 38 x 22 x 22 centimeters in size. Wood shavings were used as a substrate, hay was added as bedding material and boxes as shelters. Water (in water bottles) and food (commercial mouse breeder diet or wheat, apples etc.) were provided ad libitum.

Apparatuses and procedures used in the experiments are described further in relevant sections under Results. The animals were observed under red light illumination of low intensity (60W red bulb). All the procedures were performed blind. The first two sets of experiments (experiment I) were conducted in the summer (August 1992) when the animals were in reproductive condition, while the remaining ones (experiments II and III) were carried out during winter months (December 1992–January 1993) when majority of animals were in post reproductive condition (males with testes in partial regression at least).

## RESULTS

### Experiment I: Europe versus Far East

The experiment was designed in order to test discrimination between odours of *Apodemus agrarius* from Europe and Far East. We tested whether the animals exhibit any preference for the odour of their own or geographically related population and also whether the behavioural reaction to odour of distant population was distinguishable from the response to odour of another species or non-scented control.

**SUBJECTS** 4 males and 7 females from Far East, 3 males and 4 females from European populations (Bohemia 2 females, Slovenia 3 males and 1 female, Turkey 1 female).

**APPARATUS AND PROCEDURE** All the animals, regardless of their origin, were subjected to the same experimental design. Each animal was subjected to a single 40 minute test in an unfamiliar environment. The experiments were performed in a plastic circular arena, 100 centimeters in diameter, surrounded by a wall 60 cm high. Eight plexiglass containers (10 cm in diameter, 8 cm high) were placed regularly at a distance of 5 cm from the wall. Every container was endowed with the aperture (3 cm in diameter) which was oriented to the wall of the arena. Mixed sawdust bedding (approximately 25 ml) from the cage in which pair of animals was housed, was placed in the containers as the odour source. Each pair of opposite boxes was scented with odours of the same type (each obtained from different animals). The following four odours were simultaneously used in all tests: *Apodemus agrarius* from Europe, *Apodemus agrarius* from Far East, *Apodemus peninsulae* (outgroup) and pure wood shavings (control). The position of scented boxes was rotated from test to test. At the beginning of each testing session the animal was removed from the transport container and placed at the center of the arena. Behavioural activities were registered for the next forty minutes. Special attention was paid to the number of visits in different boxes and time spent in each. Rearing, jumping, grooming and freezing were also recorded. The floor of the arena and all the containers were thoroughly washed using 96% ethanol after each experimental session.

Table 1. Time spent in containers scented with different odours [s] and results of analysis of variance for log transformed data.

odour source	population tested			
	Europe n=7		Far East n=11	
	mean	S.E.	mean	S.E.
Europe	997	297	583	168
Far East	221	62	621	206
<i>A. peninsulae</i>	370	160	340	165
non-scented	63	17	74	30
ANOVA: odour source	F=2.86 P=0.0579		F=5.99 P=0.0018	

Results were analyzed by the means of analysis of variance (Tab. 1). Significant differences in time spent in different containers were found for mice from Far East only. However, animals of both populations spent less time in non-scented containers.

In addition we tested female preference not only for odours, but for males also. The apparatus and procedure for this experiment was similar to that of experiment II (see below). The only difference was, that each plexiglass container was divided by a metallic grating into two equal parts. In one part unfamiliar male *Apodemus agrarius* was placed. The female was allowed to enter the empty part of the container through an aperture. Choice between containers with male from Far East and Europe was allowed. Each female was tested three times (with different pair of males in each session) in order to enlarge sample. Results (Tab. 2) revealed nonsignificant preference for males of the female's own population in females from Far East ( $P=0.054$ ). No such preference was found even in females from Europe. However, the limited size of samples ought to be noted.

Table 2. Time [s] spent in containers with males of European or Far East origin.

male origin	origin of females tested			
	Europe n=12		Far East n=21	
	mean	S.E.	mean	S.E.
Europe	845	244	634	159
Far East	820	243	1172	170
Wilcoxon test	z=0.431 P=0.666		z=1.932 P=0.054	

#### Experiment II: Choice between odours from two different populations

The experiment was performed in order to test discrimination between odours of different populations of *Apodemus agrarius* coming from Bohemia, Slovenia and Far East.

**SUBJECTS.** 34 individuals of *Apodemus agrarius* from two different European populations, 16 individuals (8 males and 8 females) from Bohemian population and 18 individuals (11 males and 7 females) from Slovenia. The same animals were used in 3 successive sets of this experiment. Within each set some animals were retested in order to enlarge samples. Results of repeated tests were treated as independent items when significance of preferences was tested by non-parametric statistics. It was allowed, due to the fact, that analysis of variance performed for factors experimental set and individual animal did not revealed any significant effect of the later factor ( $d.f.=33$ ,  $F=1.30$ ,  $P=0.1436$ ) on the relative preference (percent of time spent) in sets with significant results of Wilcoxon test (Experiment II and III were pooled for this analysis of variance). Additionally four pairs of animals of Far East origin were used as odour source only.

**APPARATUS AND PROCEDURE.** Experiments were performed in plexiglass cages similar to those in which animals were housed (38 x 22 x 22 cm). Two plexiglass containers (10 cm in diameter, 8 cm high, aperture 3 cm) were placed on the floor of the cage, one to the left and another to the right side (about 5 cm from the wall). The aperture of each container was oriented to the opposite lateral side of the cage. Sawdust bedding (approximately 25 ml) from the cage in which pair of animals was housed, as the odour source was placed into containers. Each container was scented using different odour source.

The combination of animals used as odour sources was changed after each session in order to prevent any possible influence of this factor. Also the left/right position of odours was regularly changed in a balanced design.

At the beginning of each experimental session the animal to be tested was captured into a transport container, transferred to an experimental cage and immediately released exactly in the center of its floor. For the next 40 minutes the animal was observed and the time spent in the left and/or right container was recorded. After each session the cage and especially both the containers were thoroughly washed by 96% ethanol.

Times spent in containers scented with different scents were compared using nonparametric statistics (Wilcoxon test). Due to the fact that no obvious differences between the responses of males and females were found (Tab. 6), the results obtained from both sexes were pooled.

#### Related versus distant population

Sawdust bedding from two strange populations of *Apodemus agrarius*, one less and one more related served as odour sources. We tested whether *Apodemus agrarius* from Europe showed any preference for odours of animals from another European population over the odours of animals from the Far East. One container of each pair was scented with odour of *Apodemus agrarius* from the Far East, while the other one with odour of another European population, i.e., Slovenian for the testing of individuals from Bohemia and Bohemian for the animals from Slovenia.

RESULTS. Animals from both European populations spent more time in containers scented with odours of animals from another European population (Tab. 3). The differences tested using nonparametric statistics were highly significant for Slovenian ( $P=0.0058$ ) as well as for Bohemian population ( $P=0.0008$ ).

#### Own versus related population

We tested whether *Apodemus agrarius* from Europe showed any preference for odours of other animals from their own population over the odours of animals from another European population. One container of each pair was scented with odour of *Apodemus agrarius* from own population, while the other one with odour of another European population, i.e., Slovenian for the testing of individuals from Bohemia and Bohemian for the animals from Slovenia.

RESULTS. Preference for the subject's own population was not found. Animals from both populations spent more time in containers scented with odour of another European population (Tab. 3). However, this preference was significant in Bohemian population ( $P=0.0438$ ), while only nonsignificant trend was found in Slovenian population ( $P=0.2111$ ).

#### Own versus distant population

We tested whether *Apodemus agrarius* showed any preference for odours of other animals from their own population over the odours of animals from distant population. One container of each pair was scented with odour of *Apodemus agrarius* from the subject's own population, while the other one with odour of Far East (when European mice were tested) or Bohemian (for testing mice from Far East) populations.

RESULTS. Animals from all three populations spent more time in containers scented with the odour of the distant population (Tab. 3). However, while this preference was strong in the Far East population ( $P=0.0006$ ), it was only slight and nonsignificant in both European populations (Bohemian  $P=0.1023$ ; Slovenian  $P=0.2548$ ).

**Table 3** Results of experiment II. Mean time spent in containers scented with odour from two different populations, number of cases in which the animal spent more time in the container scented with the first (+) and the second source (-), and results of testing preferences using non-parametric statistics (Wilcoxon test)

animals tested	n	source 1		source 2		differences		P
		mean	S.E.	mean	S.E.	+	-	
distant vs related:								
		Far East		Slovenia				
Bohemia	25	480	99	1623	98	3	22	0.0008
		Far East		Bohemia				
Slovenia	25	620	99	1291	103	5	20	0.0058
own vs related:								
		Bohemia		Slovenia				
Bohemia	20	683	175	1562	184	6	14	0.0438
		Slovenia		Bohemia				
Slovenia	20	816	178	1298	195	7	13	0.2111
own vs distant:								
		Bohemia		Far East				
Bohemia	20	944	190	1311	202	8	1	0.1023
		Slovenia		Far East				
Slovenia	20	807	203	1340	190	7	13	0.2548
		Far East		Bohemia				
Far East	18	263	91	1782	117	1	17	0.0006

### Experiment III: Choice between scented and non-scented containers

The experimental design was similar to that used in the previous experiment. The substantial difference was that the animals were given a choice not between two conspecific odours, but between scented and non-scented containers.

**SUBJECTS.** The same as in experiment II. Each animal was subsequently subjected to following five conspecific odours in five successive sets of this experiment: Distant (= Far East population), Related (= another European population), Own (= unfamiliar animals from subject's own population), Turkey, Related (repeated test).

**APPARATUS AND PROCEDURE.** One container of each pair was scented with odour of *Apodemus agrarius* from one of population used, while the other one remained non-scented, i.e., contained pure wood shavings. Other details were the same as in experiment II.

#### Non-scented versus related population

We tested whether *Apodemus agrarius* from Europe showed any preference for containers scented with odours of animals from another European population over non-scented containers. One container of each pair was scented with odour of *Apodemus agrarius* from another European population, i.e., Slovenian for the testing of individuals from Bohemia and Bohemian for the animals from Slovenia, while the other container remained non-scented.

**RESULTS.** An apparent preference for scented containers was found (Tab. 4). The differences be-



tween mean time spent in scented and non-scented containers are parallel to those found in the first set of experiment II. The statistics was highly significant:  $P=0.0035$  and  $P=0.0040$  for Bohemian and Slovenian populations, respectively.

NOTE. This set was repeated at the end of all sets of experiment III in order to test possible influence of habituation caused by retesting. Results given in Tab. 4 indicate, that preference did not disappear.

#### Non-scented versus own population

We tested whether *Apodemus agrarius* from Europe showed any preference for odour of their own population. One container of each pair was scented with odour of unfamiliar animals from their own population, while the other container remained non-scented.

Table 4 Results of experiment III. Mean time spent in scented and non-scented containers, number of cases in which the animal spent more time in the scented container (+) and non-scented control (-), and results of testing preferences using non-parametric statistics (Wilcoxon test)

animals tested	n	source 1		source 2		differences		P
		mean	S.E.	mean	S.E.	+	-	
distant vs nonscented control								
		Far East		control				
Bohemia	16	1630	209	571	193	12	4	0.0140
		Far East		control				
Slovenia	18	137	220	891	197	11	7	0.1634
related vs nonscented control								
		Slovenia		control				
Bohemia	16	1749	175	495	168	13	3	0.0035
		Bohemia		control				
Slovenia	18	1768	166	458	167	14	4	0.0040
own vs nonscented control								
		Bohemia		control				
Bohemia	16	1406	243	843	257	10	6	0.3935
		Slovenia		control				
Slovenia	18	831	227	1352	239	6	11	0.5057
Turkey vs nonscented control								
		Turkey		control				
Bohemia	15	656	179	1567	187	3	12	0.1055
		Turkey		control				
Slovenia	19	1468	215	763	221	12	7	0.0872
related vs nonscented control (retesting)								
		Slovenia		control				
Bohemia	15	1488	204	809	201	13	8	0.0386
		Bohemia		control				
Slovenia	15	1651	223	589	215	11	4	0.0184



**RESULTS.** An apparent preference for scented containers was not found (Tab. 4). No significant differences between mean time spent in scented and non-scented containers were found. Also the mean values are very close one to another. Bohemian mice preferred rather scent of their own population, while the Slovenian ones preferred non-scented containers. We can conclude that no clear preference was detected in both populations.

#### Non-scented versus distant population

We tested the hypothesis that *Apodemus agrarius* from Europe showed preference for containers scented with odours of animals from Far East population over non-scented containers.

One container of each pair was scented with odour of *Apodemus agrarius* from Far East population, while the other remained non-scented.

**RESULTS.** As expected, no clear preference for scented container was found. Animals from both populations spent more time in scented containers (Tab.4). However, this preference was very weak. It was statistically nonsignificant in Slovenian population ( $P=0.1634$ ), while slightly significant in Bohemian population ( $P=0.0140$ ).

#### Non-scented versus Turkish population

In addition we tried also to test responses of European *Apodemus agrarius* to odour of single female from Turkey. Results given in Tab. 4 revealed nonsignificant tendency to prefer this odour over non-scented wood shavings in Slovenian population ( $P=0.0872$ ). However, larger sample of donor animals is needed for any conclusion.

Table 5 Mean time spent on the field outside containers [s] in experiments II and III NSC = non-scented

choice between odours	n	animals tested				
		Bohemia		n	Slovenia	
		mean	S E		mean	S E
distant vs related	25	296	29	25	489	53
own vs related	20	156	64	20	287	45
own vs distant	21	145	42	20	253	47
distant vs NSC	16	199	100	18	138	72
related vs NSC	16	156	30	18	174	21
own vs NSC	16	151	32	17	218	59
Turkey vs NSC	15	177	32	19	168	36
related vs NSC	21	103	16	15	160	24

Note Following corresponding values were found for Far East population tested in combination own vs distant  $n=18$ , mean=355, S E=64.

### Comment on exploratory behaviour

In all the experiments, mice from Far East and Slovenia were more exploratory than Bohemian population. As evident from Tab. 5, in six of eight sets of experiments II and III animals from Slovenian population spent more time outside containers than animals from Bohemia. Most of the time was spent actively, exploring *sensu lato*. However, evaluating these results we ought to keep in the mind that Bohemian mice were retested more frequently.

Table 6. Comparison of responses in male and female subjects in experiments II and III. Results are expressed as number of cases, in which animals spent more time in containers scented using different odour sources.

animals tested	population of odour source			
	males		females	
	distant	related	distant	related
Bohemia	1	12	2	10
Slovenia	4	10	1	10
	own	related	own	related
Bohemia	3	7	3	7
Slovenia	3	9	4	4
	own	distant	own	distant
Bohemia	3	6	5	7
Slovenia	3	9	4	4
Far East	1	8	0	9
	distant	NSC	distant	NSC
Bohemia	4	4	8	0
Slovenia	6	5	5	2
	related	NSC	related	NSC
Bohemia	8	0	5	3
Slovenia	8	3	6	1
	own	NSC	own	NSC
Bohemia	5	3	5	3
Slovenia	3	7	3	4
	Turkey	NSC	Turkey	NSC
Bohemia	3	4	0	8
Slovenia	6	5	6	2
	related	NSC	related	NSC
Bohemia	4	3	5	3
Slovenia	6	3	5	1

NSC = non scented

## CONCLUDING REMARKS AND DISCUSSION

The results of all three experiments could be summarized as follows:

1) Containers scented with odours of animals from related populations were preferred over non-scented containers as well as over containers scented with odours of conspecifics from distant population (Fig. 1). These preferences proved to be highly statistically significant in all cases. These odours were also preferred over odours of unfamiliar animals from subject's own population. Although, this preference was apparent in both populations tested, it was significant in one of them only.

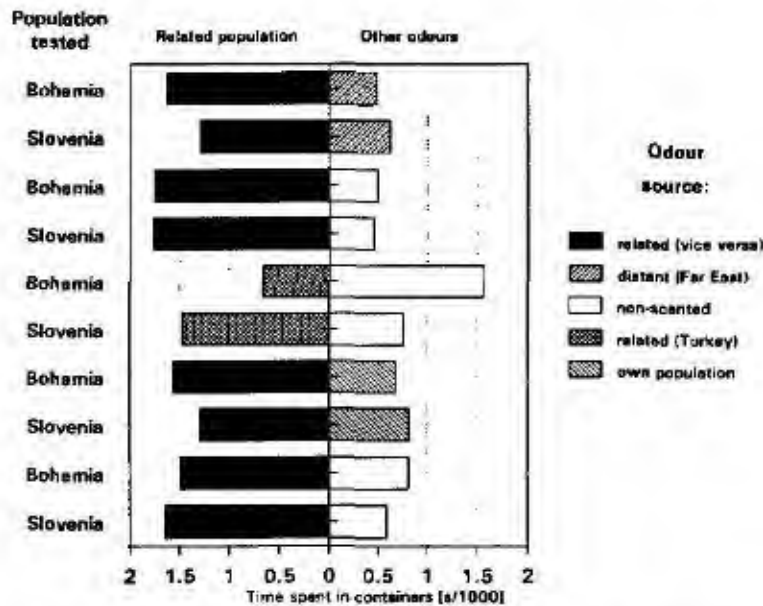


Fig. 1. Results of pair-choice tests: Means for time spent in containers scented with odour of related population compared with those spent in simultaneously exposed containers scented with another scent.

2) Animals of all populations under study spent more time in containers scented by odours of animals from distant populations than in those scented with odours of unfamiliar conspecifics from their own population or in non-scented containers (Fig. 2). These preferences were found to be nonsignificant or slightly significant in European populations and once nonsignificant (experiment I) and once highly significant (experiment II) in animals from Russian Far East.

3) Containers scented by odours of unfamiliar animals of their own population were not preferred in any case when given choice. The only exception are the animals from Bohemian population, which spent slightly and nonsignificantly more time in containers scented with odours of their own population than in non-scented containers (Fig. 2). Evaluating these results one should remark, that greater mean body weight is typical for the Far East subspecies of *Apodemus agrarius* (Vinogradov & Gromov 1952). In accordance with this trend also our experimental animals belonging to this subspecies were in general heavier than their conspecifics from Europe. Possible

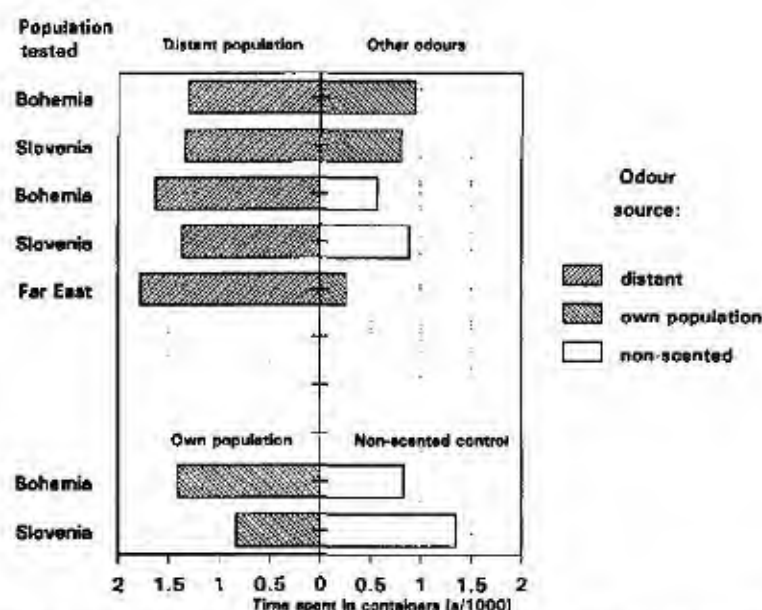


Fig. 2. Results of pair-choice tests: Means for time spent in pairs of simultaneously exposed containers scented with different odours. Comparisons in which odours of related populations were not included.

influence of this fact on the choice experiment could not be simply excluded.

Odours used in experiments were obtained from pairs of animals and no clear differences between male and female responses to these odours were found (Tab. 6). Considering this fact as well as winter period's influence, in which the experiments II and III were performed, we can conclude that motivation of the animals were probably rather social investigatory than sexual.

Our results showing that Stripped-field mice prefer conspecific odours of medium relatedness can be easily attributed to attraction of new stimuli placed in a familiar context, that seems to be a general rule caused by organisation of cognitive apparatus. Similar pattern of preferences was found also in kin discrimination, e.g., mate choice favouring cousins in Japanese quails (Bateson 1982). However, simple proximate explanations are not fully sufficient and underlying ultimate causes (e.g., advantage of outbreeding combined with risk of interspecific hybridisation) ought to be found.

#### Acknowledgements

We thank the referee Prof Dr D. A. Dewsbury (Gainesville, U.S.A.) for his critical comments, valuable suggestions and improvement of the English. We express our great appreciation to Dr Boris Kryštufek (Ljubljana, Slovenia) and Mgr Karel Weidinger (Prague) for kindly donating wild-caught *Apodemus agrarius* from Slovenia and Russian Far East, respectively. We also thank Prof Dr Ivan Vyskočil (Prague) for his kind support in catching the animals in village Chřibská.

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**Intraspecific behavioural interactions in the Striped-field mouse (*Apodemus agrarius*)  
and its interspecific relationships to the Wood mouse (*Apodemus sylvaticus*): dyadic  
encounters in a neutral cage**

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Received January 30, 1994; Accepted February 9, 1995

Published June 22, 1995

**Aggressive behaviour, interspecific competition, behavioural ecology, *Apodemus***

**Abstract.** Intraspecific male-male, female-female and male-female interactions of *Apodemus agrarius* as well as interspecific interactions between this species and a possible competitor *A. sylvaticus*, were video-recorded and subsequently analysed. Altogether, 89 neutral cage dyadic encounters each lasting 10 minutes were performed. In both intraspecific and interspecific tests, male-male interactions were markedly and significantly more agonistic than the female-female ones. Females were subordinate in male-female interactions. Superiority of *A. agrarius* over *A. sylvaticus* was found in most interspecific interactions.

#### INTRODUCTION

The Striped-field mouse, *Apodemus agrarius* (Pallas, 1771), is a common rodent in the eastern part of Europe (Böhme 1978). Despite its vast range extending from Eastern Asia to Europe (Kratochvíl et al. 1976, Corbet 1978) and noticeable representation in small mammal communities (Karaseva et al. 1992), no substantial attention has been paid to its social behaviour.

This study is a part of research program involving comparative behavioural studies of Palaearctic mice (Frynta 1992a, 1994, Čiháková & Frynta in prep.). It was conducted to enhance comparative information on behavioural patterns in intraspecific and interspecific interactions involving *Apodemus* species. For this purpose, a simple procedure of dyadic encounters in neutral cage permitting quantification of the behavioural elements in a standardised test was adopted. This procedure is used widely in studies of rodent behaviour and despite the limitations discussed below, remains a useful tool for interspecific studies.

The relevance of simple laboratory experiments performed in a clean, neutral cage of small size to natural situation, is questionable. There are studies suggesting that behavioural interactions are situation dependent. Intraspecific interactions may be influenced, e.g., by scent marks as described by Hurst (1993) in *Mus musculus domesticus*. It is also reported that under some circumstances, dominance in interspecific interactions involving *Peromyscus maniculatus* and *P. leucopus*, is more dependent on residence than on species (Wolff et al. 1983).

The following questions concerning behavioural ecology of *Apodemus* species were addressed: 1) Are the levels of intermale aggression high enough to explain elimination of male *A. agrarius* reported in studies of natural populations? 2) What is the role of direct aggression in competitive interactions between *A. agrarius* and *A. sylvaticus*?



## MATERIALS AND METHODS

**Subjects.** In total, 31 sexually mature and socially experienced specimens of Striped-field mouse (*Apodemus agrarius*) coming from following two different populations were under the study.

1) Northern Bohemia (Czech Republic). Fourteen individuals (8 males and 6 females) captured in the village of Chřibská (district Děčín) in October 1992. 2) Slovenia (part of former Yugoslavia). Sava River valley near the town of Brežice (Eastern Slovenia). Four individuals (3 males and 1 female) captured in July 1992, nine animals (4 males and 5 females) captured in August 1992, four males born in the laboratory in late August 1992.

Both populations used in our experiments, as well as most other European populations, are considered to belong to a single subspecies *Apodemus agrarius agrarius* (Pallas, 1778).

At the time of testing intraspecific encounters, the mean body weights of *A. agrarius* (populations pooled) were 29.4 g (min 23.0 g, max 41.9 g) and 23.4 g (min 16.6 g, max 31.5 g) in males and females, respectively.

The opponents used for interspecific interactions were 29 individuals (17 males and 12 females) of Wood mice, *Apodemus sylvaticus* (Linnaeus, 1758). They were wild born, sexually mature and socially experienced animals captured in autumn 1992 at various localities in Prague (Central Bohemia) and maintained in the laboratory throughout the subsequent winter and spring until testing. Their mean body weight was 23.6 g (min 16.0 g, max 32.8 g) and 21.6 g (min 17.7 g, max 32.3 g) in males and females, respectively. The corresponding values for *A. agrarius* used in the interspecific encounters were 32.2 g (min 25.5 g, max 44.0 g) and 27.2 g (min 17.3 g, max 34.5 g).

In order to control the effect of differences in body weight between *A. agrarius* and *A. sylvaticus*, dyads were set together as follows. Experimental subjects of the former species were arranged in ascending order according to their body weight, while individuals of the later species were tested in descending order according to that variable. This scheme allowed us to create continual sequence of dyads starting from *A. sylvaticus* greater than *A. agrarius* through the balanced dyads to the opposite relation at the end.

**Housing conditions.** All animals were kept under an artificial 16L: 8D light cycle and housed by pairs in plastic cages 38 x 22 x 22 cm in size. Wood shavings were used as a substrate, hay was added as bedding material and boxes as shelters. Water in water bottles and food (commercial mouse breeder diet or wheat, apples etc.) were provided ad libitum.

**Apparatus and procedure.** Encounters between mice were performed in a 50 x 30 x 35 cm glass cage. The cage was divided by thick card partition into two equal parts. During testing the cage was illuminated by a single 40 W red light bulb suspended in the distance approximately 1.5 meters. Mice were tested during the dark phase of their light-dark cycle. At the beginning of each experimental session two mice were placed in the pen, one on either side of the partition, and left for five minutes. The central partition was then removed and video recording by single VHS-camera commenced. The video camera was stopped at the end of the session, i.e., ten minutes after the moment when one or both animals for the first time paid attention to the other. After each session sawdust covering the floor was changed and the cage was thoroughly cleaned using 96% ethanol.

In total, 87 encounters arranged in three successive sets, were recorded. Intraspecific male-male and male-female encounters (20 for each sex) were performed in the first, intraspecific male-female in the second (20 encounters), and the interspecific ones (17 male-male, 12 male-female) in the third set. In the intraspecific encounters, one half of the encounters was performed with Bohemian and the second half with Slovenian animals. Both animals of each dyad were of the same geographical origin. Each animal was tested with different opponents 2-4 times in the first, and 1-2 times in the second, and only once in the third set. Repeated testing of the same individual was not performed earlier than 24 hours after the preceding test. No effect of multiple testing was evident.

The first two sets of experiments were carried out in spring (April 1993), while the third was carried out in summer (August 1993).

**Behaviour elements and their classification.** For purposes of data collection the behaviour was divided into 33 elements, which were with minor changes adopted from similar studies in *A. sylvaticus* (Gunnell 1977, Montgomery 1978). Detailed description of individual elements is given in Čiháková & Frynta (in prep.). The elements were subsequently summarised into 18 secondary categories defined and classified into 5 functional blocks as following.

(A) Agonistic: (I) Threat attack, (II) Chase, (III) Roll-over fight, (IV) Box, (V) Neutral upright, (VI) Ambivalent, (VII) Defensive (upright or threat), (VIII) Avoid retreat, (IX) Flee-freeze, (X) Submissive. (B) Introductory: (I) Attend, (II) Approach, (III) Nose. (C) Amicable: (D) Individual: (I) Self groom, (II) Crouch-sit. (E) Exploratory: (I) Loco-explore, (II) Rear-jump.

Note: Categories A/ I - II are denoted as aggressive, A/ III - VI as neutral, and A/ VII - X as defensive.

**Methods of data collection.** Video records of encounters were subsequently observed and analysed. Observed behavioural elements were quantified using the computer program package ACTIVITIES (Viha & Donát 1993). Data on total duration of each element for a particular session and animal, were used as primary data for further analysis. Duration was expressed in seconds. Sums of time for both individuals in a dyad were used to characterise each type of encounters.

In dyads where non-neutral, agonistic interactions were recorded, the animal displaying the higher value of an index of dominance was classified as the winner of the encounter. The index of dominance was calculated as sum of time spent by dominant and aggressive behaviour (A/I, II) minus sum of time spent in agonistic behaviour considered to be defensive or submissive (referred further as defensive, A/ VII, VIII, IX, X).

No substantial differences were found between the results obtained in animals of different geographical origin. However, differences between populations in male-male interactions were slight and not significant. Four laboratory born males from Slovenia did not behave differently from wild caught mice. General accordance between behavioural patterns displayed by different populations were found also in female-female encounters, although Slovenian mice exhibited significantly more agonistic (means: 77.4 and 15.4 s;  $P=0.004$ ) and less individual (means: 594.1 and 781.9 s,  $P=0.023$ ) behaviour than Bohemian mice. Despite this difference, results obtained for Bohemian and Slovenian mice were pooled for further analyses.

It has to be noted here that experiments were performed in individual sets that are comparable to a limited extend only. This is due to possible sequence bias and also effect of the season. Therefore, statistical evaluations and interpretations of the results were exclusively based on within set comparisons.

## RESULTS

### Intraspecific interactions

Percentage of time spent in main behavioural categories in different type of encounters are illustrated in Figs 1-2. Means for time spent by individual categories of behavioural elements are presented in Tab. 1.

Sexual differences were apparent. All categories of agonistic behaviour were more evident in male-male than in female-female interactions. Testing of these sexual differences by non-parametric statistics (Mann-Whitney U-test) showed that majority of sex differences were highly significant (Tab. 1). Male-male interactions were also characterised by significantly smaller amounts of amicable ( $P=0.0121$ ) and individual behaviour ( $P=0.0275$ ).

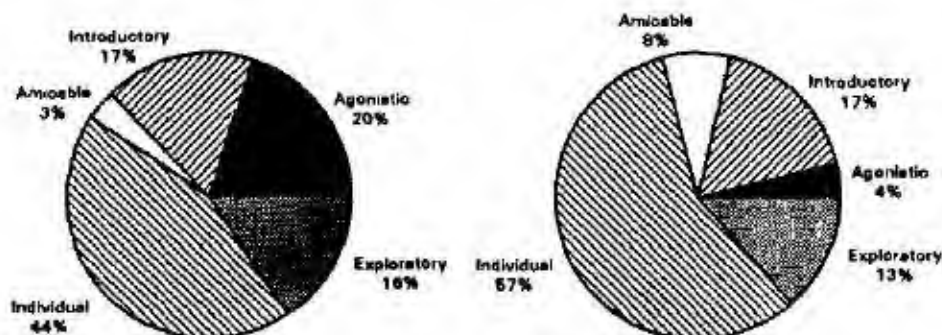


Fig. 1. Percentage of time spent in different types of behaviour in male-male (left;  $n=20$ ) and female-female (right;  $n=20$ ) intraspecific encounters of *A. agrarius*.

Table 1 *Apodemus agrarius*. Mean duration (in seconds) of different behavioural categories and significance of differences between sexes in intrasexual and intersexual encounters as revealed by non-parametric statistics. Mann-Whitney = unpaired U-test, Wilcoxon = paired signed-rank test; n = number of dyads

Sex	Intrasexual encounters			Intersexual encounters			Wilcoxon
	Male- male n=20	Female- female n=20	Mann-Whitney  P	Male- female n=20	contribution of males females		
threat-attack	54.3	6.4	0.0003 ***	14.6	13.9	0.7	0.0382 *
chase	18.3	2	0.0005 ***	7.2	7.2	0	0.0310 *
roll-over flight	18.3	6	0.0001 ***	9.8	5.5	4.3	0.2084
box	2.8	2.0	0.1448	1.6	0.4	1.2	0.3711
neutral upright	18.1	6.2	0.0754	8.1	4.1	4.0	0.5294
ambivalent	12.9	4.3	0.0367 *	1.4	1.1	0.3	0.1814
defensive	76.9	16.9	0.0042 **	46.3	3.2	43.1	0.0068 **
avoid-retreat	11.4	9.1	0.4794	8.7	4.3	4.4	0.4534
flee-freeze	22.3	0	<0.0001 ***	8.0	0.0	8.0	0.0225 *
submissive	3.1	7	0.0728	2.3	0	2.3	0.0736
AGONISTIC	238.2	46.4	0.0006 ***	108.1	39.8	68.3	0.0149 *
standard error	41.4	12.9		32.6	12.4	21.0	
attend	67.9	54.7	0.3369	29.3	8.7	20.6	0.0177 *
approach	20.3	17.2	0.3648	18.3	8.8	9.5	0.3603
nose	117.5	137.0	0.4903	157.3	85.3	72.0	0.1403
INTRODUCTORY	205.7	208.8	0.7972	204.8	102.8	102.0	0.9851
standard error	12.8	23.3		16.6	10.3	9.7	
AMICABLE	41.8	92.5	0.0121 *	139.6	44.5	95.1	0.0294 *
standard error	17.5	22.8		40.1	20.1	26.9	
selfgroom	181.3	157.4	0.7557	178.8	93.1	85.7	0.5628
croach-sit	342.1	530.7	0.0023 **	344.6	182.1	162.5	0.7795
INDIVIDUAL	523.4	688.0	0.0275 *	523.3	275.1	248.2	0.8666
standard error	43.0	40.8		40.5	27.2	28.9	
loco-explore	131.8	108.7	0.5250	167.4	108.2	59.2	0.0130 *
rear-jump	55.9	52.6	0.9031	56.6	29.6	27.0	0.8960
EXPLORATORY	187.7	161.3	0.6359	224.1	137.8	86.3	0.0239 *
standard error	25.7	18.4		28.7	18.7	20.1	

Males were classified as dominant in 13 of 18 male-female dyads in which dominant or defensive behaviour was recorded. Threat-attack as well as chase, i. e. signs of dominance, were displayed almost exclusively by males in these encounters, while females spent more time in defensive behaviour (Tab. 1). Females also displayed significantly more amicable ( $P=0.0294$ ) and less exploratory behaviour ( $P=0.0239$ ).

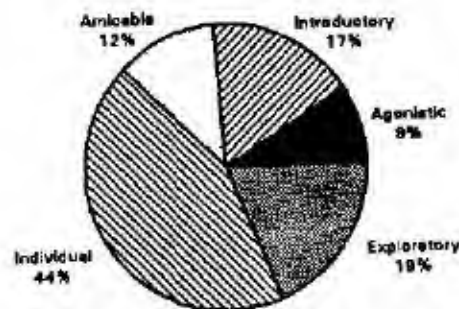


Fig. 2. Percentage of time spent in different types of behaviour in male-female ( $n=20$ ) intraspecific encounters of *A. agrarius*.

### Interspecific interactions

Behavioural patterns displayed in interspecific encounters generally resembled those found in intraspecific ones (Tab. 2, Fig. 3). The only apparent difference was the low incidence of amicable behaviour.

Male-male interspecific encounters were more agonistic than female-female ones (Mann-Whitney unpaired test  $P=0.0253$ ), but the differences were less pronounced than in intraspecific encounters (Tab. 2).

Mean behavioural patterns of each species in interspecific encounters are presented in Tab. 2. *A. agrarius* initiated almost all the agonistic interactions recorded in interspecific tests. It was frequently but not necessarily always the winner in these dyadic encounters. Using the index of dominance (see Materials and methods), this species was classified as the winner in 20 of 29 encounters (males: 11 of 17; females: 9 of 12). In males this superiority of *A. agrarius* appeared to be significant ( $P=0.0231$ ) when tested by non-parametric statistics (Wilcoxon matched pairs signed test). The ratio between the body weights of interacting animals is slightly correlated with defensive behaviour but remains not correlated with dominant behaviour recorded in the encounter (Fig. 4).

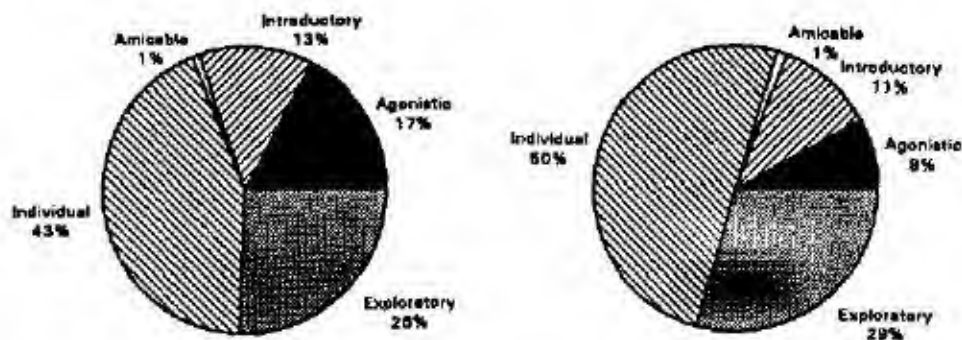


Fig. 3. Percentage of time spent in different types of behaviour in male-male (left;  $n=17$ ) and female-female (right;  $n=12$ ) interspecific encounters between of *A. sylvaticus* and *A. agrarius*.

Table 2 Mean duration (in seconds) of different behavioural categories and significance of differences between species in interspecific encounters as revealed by non-parametric statistics (Wilcoxon matched pairs signed rank test)

Species Sex	<i>A. sylvaticus</i> versus <i>A. agrarius</i>				Females n=12			
	Males n=17	A sy	A ag	Wilcoxon P		A sy	A ag	Wilcoxon P
threat attack	30.8	2.5	28.2	0.0248 *	9.8	2.1	7.7	0.3627
chase	16.6	2.3	14.3	0.0253 *	5.0	1.5	3.5	0.2945
roll-over fight	4.2	1.9	2.3	0.4069	1.2	1.1	1	0.3710
box	5.3	3.1	2.2	0.0590	4	0	4	0.0455 *
neutral upright	7.9	4.1	3.8	0.7998	14.8	4.8	10.0	0.0759
ambivalent	14.7	10.6	4.1	0.7262	8.1	2	7.9	0.7961
defensive	58.8	46.5	12.3	0.2329	26.7	11.1	15.6	0.9056
avoid retreat	22.8	11.7	11.1	0.5540	19.3	13.1	6.2	0.0376 *
flee-freeze	38.4	31.1	7.3	0.0332 *	11.0	7.1	3.9	0.1235
submissive	6.0	5.9	1	0.0225 *	3	3	0	0.0455 *
AGONISTIC	205.5	119.8	85.7	0.1359	96.7	41.3	55.4	0.1955
standard error	37.0	22.6	18.7		15.7	7.3	10.8	
attend	35.9	19.7	16.2	0.6529	27.4	14.4	13.0	0.9687
approach	15.4	6.8	8.6	0.3437	15.5	3.7	11.8	0.0233 *
nose	105.9	47.7	58.2	0.2096	91.5	37.6	54.0	0.0559
INTRODUCTORY	157.1	74.2	82.9	0.5383	134.4	55.6	78.8	0.0207 *
standard error	14.7	11.3	7.5		24.1	11.9	14.0	
AMICABLE	9.9	3.1	6.8	0.4185	14.1	12.9	1.2	0.0614
standard error	5.4	1.5	4.7		8.8	8.1	8	
selfgroom	238.9	100.5	138.3	0.1850	205.5	73.2	132.3	0.0454 *
croach-sit	281.0	151.0	130.0	0.7763	397.7	243.0	154.8	0.1078
INDIVIDUAL	519.9	251.5	268.3	0.4777	603.2	316.2	287.1	0.2896
standard error	36.2	25.4	26.8		67.5	41.1	34.6	
loco-explore	253.7	117.5	136.2	0.7763	281.6	133.2	148.4	0.6101
rear-jump	53.7	33.8	19.8	0.1929	68.3	40.6	27.6	0.2895
EXPLORATORY	307.4	151.3	156.1	0.8498	349.9	173.8	176.1	0.9687
standard error	30.8	23.8	21.0		52.3	34.3	27.9	

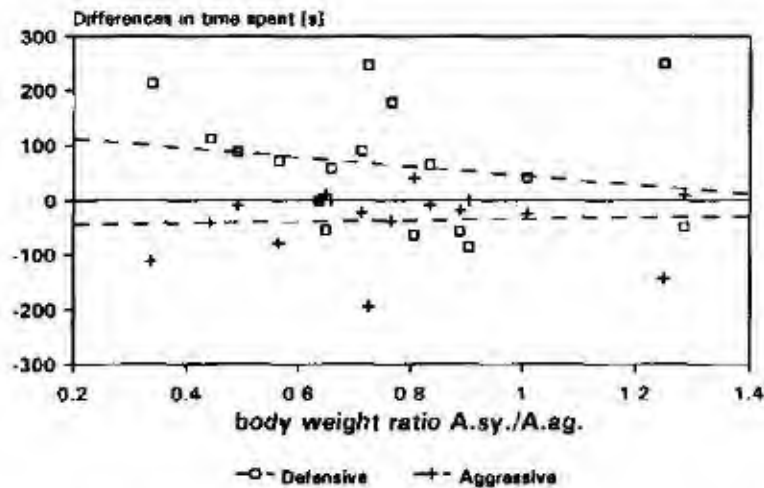


Fig. 4 Relationship between the dominance and body weight in interspecific male-male encounters of *A. sylvaticus* and *A. agrarius*. Ordinate: differences between behavioural parameters (time spent by defensive or aggressive elements) recorded for *A. sylvaticus* and *A. agrarius* in individual dyads. Abscissa: body weight ratio between *A. sylvaticus* and *A. agrarius* within the dyad.

## DISCUSSION

### Intraspecific Interactions

Our results suggest that male *A. agrarius* are more aggressive than females. The difference between sexes was much more apparent than differences between individual populations found in female-female interactions. This is in a general agreement with published data on behaviour of other *Apodemus* species (Richard-Yris 1979, Bovet 1972 a,b, Gurnell 1977, Montgomery 1978, Čiháková & Frynta in prep.).

Behavioural patterns displayed by *A. agrarius* in our experiments can be compared with results of 10 minute dyadic encounters that were performed in our laboratory using almost identical procedure in *A. sylvaticus* and *A. flavicollis* (Čiháková & Frynta in prep.). In this comparison, *A. agrarius* males spent on average, more time in agonistic behaviour (20% of time) than *A. sylvaticus* males (10%) and even the generally aggressive *A. flavicollis* males (16%). Taking into account that 3% of time was spent in amicable behaviour in *A. agrarius*, contrasting to 0.3% in *A. flavicollis*, we conclude that *A. agrarius* males were as aggressive as *A. flavicollis*. Females of all the species spent a much smaller proportion of time in agonistic behaviour and show little variation between species, 4% in *A. agrarius*, 5% in *A. sylvaticus* and 4% in *A. flavicollis*. The corresponding values for amicable behaviour were 8%, 8% and 6%, respectively.

The mentioned relatively high level of aggression in males of *A. agrarius* is in accordance with findings of authors studying the ecology of natural populations of this species. Bujalska (1981) described intrinsic regulation of population size in populations exceeding a density of about 50 individuals per hectare. This regulation was accompanied by the delay of sexual maturity and changes in the sex ratio resulting in an extremely low proportion of males (13.5%), at high densities of about 90 individuals per hectare. Unbalanced sex ratio has stimulated appearance of the hypothesis suggesting selective elimination of males as a result of social interactions (Pelikán



1965). Although our results suggest a high level of intermale aggression in *A. agrarius*, we have no direct evidence that elimination of males observed in nature may be attributed to this cause. In contrast, unlike in some other mice species, e. g. *A. flavicollis*, *M. macedonicus* (Frynta unpubl.), there is no strict mutual exclusion of sexually mature males in captivity. According to our long-term experience with *A. agrarius*, two or more unrelated males can be maintained under some circumstances in a single cage. Formation of aggregations has also been reported from natural populations of *A. agrarius*, but this phenomenon is found only in the winter period and may be attributed to a decreased level of aggression under non-reproductive conditions (Kosoř 1984).

### Interspecific interactions

Interspecific behavioural interactions have been repeatedly studied in small rodents, and their importance in ecological relationships between species has been proposed (Andrzejewski & Olszewski 1963, Grant 1970, Randall 1978, Dienske 1979, Cassang 1982, 1984, DeJonge 1983, etc.).

Our results suggest superiority of *A. agrarius* over *A. sylvaticus* in aggressive interactions. This fits well with the ecological patterns of their distribution. Habitat requirements of *A. agrarius* in Europe are specific (Zejda 1967, Kratochvíl 1977, Bohme 1978) but they overlap partially with those of *A. sylvaticus*. In sympatric populations, these two species occur even in the same community. However, there are some indications of their competitive interaction leading to exclusion of *A. sylvaticus*. For example, both species are able to penetrate into isolated parks or cemeteries inside large cities and to establish dense populations representing even more than 90% of the total rodent community. Within sympatry, it is regularly *A. agrarius* that forms such urban populations while the *A. sylvaticus* remains poorly represented (Chudoba et al. 1961, Andrzejewski et al. 1978, Elvers & Elvers 1984, Gavrilenko 1970, Gliwicz 1980, Mořanský 1985). In the absence of *A. agrarius*, this niche is occupied by *A. sylvaticus* (Yalden 1980, Pelikán et al. 1983, Vohralík & Řeháková 1985, Dickman & Doncaster 1986, Frynta 1992b).

Dominance of *A. agrarius* as a more specialised species, is in accordance also with a general rule operating in competitive interactions (Hallett et al. 1983). *A. sylvaticus* was found to play a role of subordinate species also when interacted with closely related species and its possible competitor *A. flavicollis* (Hoffmeyer 1973, Montgomery 1978, Čiháková & Frynta, in prep.). Smirín & Shilova (1989) reported that Wood mice are subordinate also to the House mouse (*Mus musculus*), however, the taxonomic status of Russian Wood mice is still unclear.

### Acknowledgements

We thank Prof. Dr W. I. Montgomery (Belfast, U.K.) for his critical comments, valuable suggestions and improvement of the English. We express our great appreciation also to Dr Boris Kryštufek (Ljubljana) for kindly donating wild caught *Apodemus agrarius* from Slovenia. We also thank famous writer Prof. Dr Ivan Vyskočil (Praha) for his kind support in catching the animals in village Chřibská.

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**Distribution and shell colour and banding polymorphism of the *Cepaea* species in Bohemia (Gastropoda: Helicidae)**

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Received February 1, 1995, accepted February 9, 1995  
Published June 22, 1995

**Geographic distribution, polymorphism, area effects, selection, climate, *Cepaea hortensis*, *Cepaea nemoralis*, *Cepaea vindobonensis*, Bohemia**

**Abstract.** The distribution of the local populations of *Cepaea hortensis* (Müller), *C. nemoralis* (Linnaeus), and *C. vindobonensis* (Férussac) in Bohemia and frequency of colour and shell banding morphs were recorded in 1987 - 1994. The species differ in their habitat preferences and geographic distribution. While *C. hortensis* occurs at both urban and country localities over the whole Bohemia, *C. nemoralis* is limited to urban localities of northern, central and eastern Bohemia and *C. vindobonensis* lives at steppe localities along the Labe river and its major tributaries, and in the Central Bohemian Karst. The frequency of pink morph in local populations of both species varied between 0 and 100 percent and was higher in *C. nemoralis* than *C. hortensis* populations. In both species the distribution of populations with high frequency of yellow or pink morphs is mosaic, and the same mosaic pattern has distribution of 00000 and 12345 morphs. High frequency of shell banding morphs 00300 and 00345 in *C. nemoralis* is limited to small areas. In both species there was no relationship between the above sea level altitude of the locality and percentage of pink or melanic individuals in local populations. *C. vindobonensis* populations of Bohemia show little variation.

INTRODUCTION

The presence of three *Cepaea* species, *C. hortensis* (Müller), *C. nemoralis* (Linnaeus), and *C. vindobonensis* (Férussac) in Bohemia was established since the beginnings of a scientific interest in malacology. The results of earlier works were summarized by Ložek (1956) who reviewed several papers concerning the *Cepaea* species (e.g. Slavík 1865, Petržok 1943, Sobotka 1945). Later on, distribution and variation in *Cepaea* species were not studied in detail except the work of Schilder & Schilder (1957) which marginally concerns the territory of Bohemia. Some results were published from surrounding areas of Central and Southern Europe (Jones 1973b, Rafiński 1981).

Earlier studies revealed the differences in geographic distribution of Bohemian *Cepaea* species. While *C. hortensis* populations were found at the whole territory other species were limited to some areas. *C. nemoralis* was found only in the north of the country and in several towns of western and central Bohemia (Karlovy Vary, Litoměřice, Nový Bydžov), and *C. vindobonensis* was limited to lowland surroundings of the river Labe and its major tributaries, and the karst areas of central Bohemia. The authors also mentioned typical differences in species requirements for habitat quality. Although the occurrence of colour and shell banding morphs was well documented, a systematic study of their frequencies in local populations was not undertaken. Honěk (1995) studied local distribution and shell colour and banding polymorphism of *C. nemoralis*. This work revised earlier results and presented some speculations on the causes of local differences in distribution patterns of *C. nemoralis* and *C. hortensis*.

The aim of this paper is to present a summary of distribution and variation of *C. hortensis* and publish the data on morph frequencies in local populations of *C. hortensis* and *C. nemoralis*. These data could provide a basis for the study of temporal changes in geographic distribution and polymorphism which may take an important part in determining the patterns of local morph variation (cf. Currey et al. 1968, Wall et al. 1980). Habitat preferences of the species are also discussed.

#### MATERIAL AND METHODS

*Cepaea nemoralis* and *C. hortensis* were collected systematically at the whole territory of Bohemia, in 1987-1994. Northern Bohemia was investigated with a particular intensity due to simultaneous occurrence of both species. On many localities brief visits enabled only investigating the most convenient habitats - roadsides, shrubs, urban ruderal areas and cemeteries (the latter were particularly convenient for all *Cepaea* species). The above sea level altitude of the localities was read from 1:50,000 maps. The geographic position of the localities (Appendices I and II) is indicated with respect to a reference grid used for faunistic mapping of the country (Novák 1989) which is identical with the one used for floristic research in Central Europe (Slavík 1971). The surface of the country is divided into rectangles. Their west-east dimension is 10' geographic longitude and north-south dimension is 6' geographic latitude (approximately 11 x 12 km). The rectangles are designated in the west-east (longitudinal) direction by serial numbers beginning with 38 (easterly of 12°00' E), and in the north-south (latitudinal) direction by serial numbers beginning with 49 (southerly of 51°06' N). Each rectangle is indicated by an apposition of its longitudinal and latitudinal serial number.

The colour and shell banding forms were scored in adult living animals and well preserved dead shells. The localities where >10 *C. nemoralis* or >20 *C. hortensis* individuals were collected were considered for statistic evaluation. The difference was made due to importance of *C. nemoralis* data from marginal populations. These data are included in the Appendices I and II. The colour of the shells was classified as "yellow" or "pink". In several populations the colour of some individuals was so pale that distinguishing of yellow and pink forms was difficult. In this case individuals with a trace of the pink colouration (usually near the top of the shell) were classified as "pink", the rest was classified as "yellow". The shell banding morphs were classified according to generally accepted conventions. The bands are designated as 1 to 5 beginning from the dorsal side, and a fusion of bands was indicated by brackets. As the number of fused bands could increase with animal age the number of fusions was counted at 1/4 whorl from the shell outlet. The duplicated bands (rare) were censused as single ones. "Hyalozonate" individuals whose bands were replaced by pale blanks (frequent in some *C. hortensis* populations) and individuals whose bands were diffuse (lacking the sharp edges) were censused as corresponding banded morphs. In total, 417 populations of *C. hortensis* at 343 geographic localities, 220 populations of *C. nemoralis* at 136 localities, and 35 populations of *C. vindobonensis* were sampled.

#### RESULTS

##### 1. Habitats

In Bohemia, all *Cepaea* species live at urban sites as well as at country habitats little affected by human activity. The populations were most often encountered at (1) urban habitats - street margins, parks etc., (2) cemeteries and (3) country habitats - grassy stands, shrubs, hedgerows, roadsides and other structures created by human activity.

Typical preferences of the *Cepaea* species differ largely. The main differences were (1) tendency to colonize urban or country habitats, (2) the type of vegetation cover, and (3) the altitude of the locality (Fig. 1).

*C. hortensis* is most tolerant in its requirements for habitat quality. The species lives at habitats grown by broad leaved and grassy herbs, as well as in the understory of shrubs. It was encountered at both urban (61 % of cases) and country (39 %) localities (cemeteries were not included). The species was distributed evenly from lowland (160 m a.s.l.) to submontane (740 m a.s.l.) areas.

*C. nemoralis* inhabits mostly localities grown by broad-leaved weedy stands and understory of shrubs. It occurs scarcely at places grown by grassy vegetation. Most localities were within urban areas and only a small fraction (1 %) were the roadsides in the near surroundings of the towns.



Tab 1 Graf 1

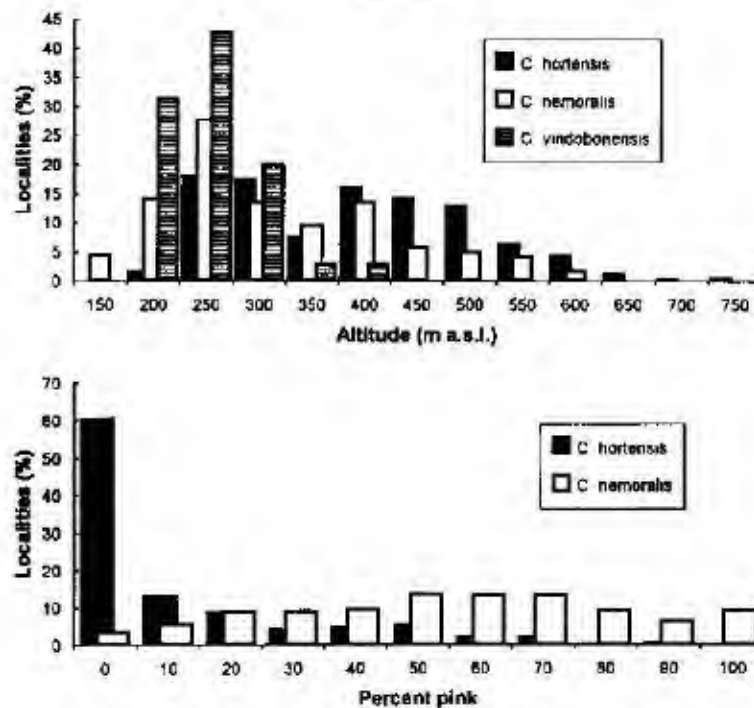


Fig. 1 Above: Altitudinal distribution of Bohemian localities of the *Cepaea* species. Below: Frequency of *C. hortensis* and *C. nemoralis* populations according to the percentage of the pink form

The populations were found over a wide altitudinal range (140 - 580 m a.s.l.), mostly below 450 m a.s.l.

*C. vindobonensis* lives at grassy steppe localities and at ruderal areas grown by mixed dicotyledonous and grass stands. Most localities were in the country (93 %). The species was found at lowland localities between 170 and 400 m a.s.l.

## 2. Geographic distribution

The three *Cepaea* species in Bohemia differ in their patterns of geographic distribution. Populations of *C. hortensis* were found, with notable exceptions, over the whole territory (Fig. 2). They were absent in montane areas bordering Bohemian frontiers - Novohradské hory, Šumava, Český les, Lužické hory, Iizerské hory, Krkonoše, Broumovské stěny and Orlické hory Mountains. The populations were apparently absent (or very scarce) also at some areas of 400 - 700 m a.s.l. altitude. This concerns the northwest of the country - Džbán, České Středohoří and Labské pískovce Hills, and Slánská tabule and Podkrušnohorská pánev Plains. An area where *C. hortensis* populations were also not found is the Brdy Mountains, the north of Plzeňská pahorkatina Hills, and Tepelské vrchy, Doupovské vrchy and Slavkovský les Mountains. *C. hortensis* populations are also less frequent in the areas where this species is replaced (at some localities) by *C. vindobonensis* and *C. nemoralis*.



*C. nemoralis* populations (Fig. 2) were found in northern Bohemia. The areas where they occupied the majority of the convenient urban sites were (a) the north of the country (bordered by Labské pískovce, Česká středohoří, Polomeň hory, Ralsko-bezděžská tabule, Český ráj, and Jizerské hory Mountains), and the towns of (b) Litoměřice and (c) Nový Bydžov with their near

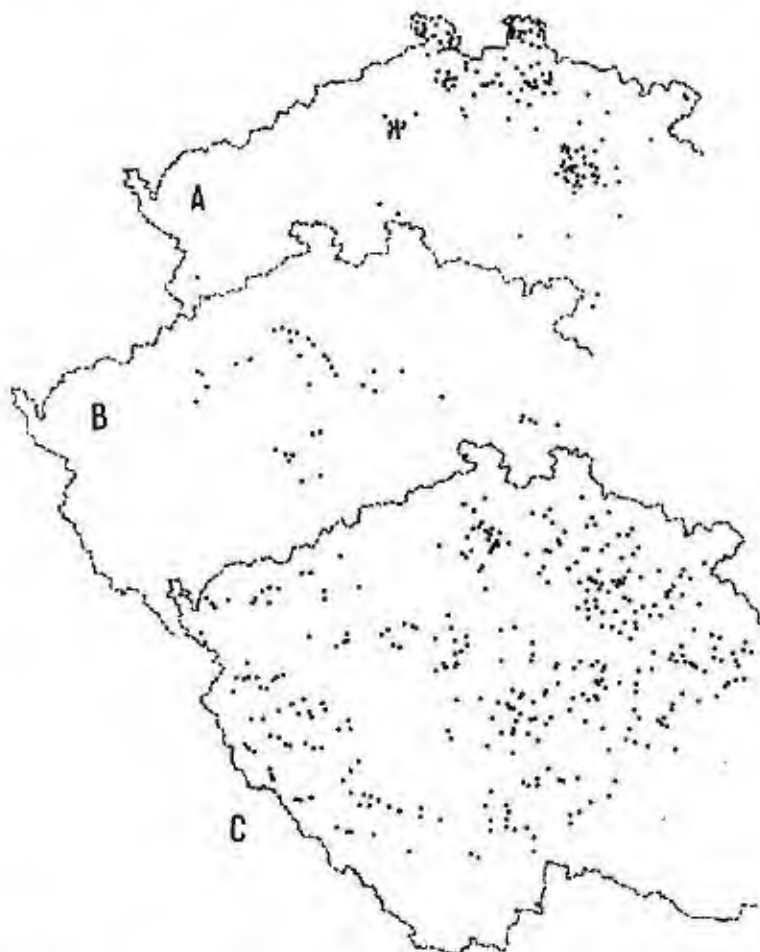


Fig. 2. Geographic distribution of (A) *C. nemoralis*, (B) *C. vindobonensis*, and (C) *C. hortensis* populations.

surroundings. In between these areas, *C. nemoralis* populations occurred at some urban localities but other ones were populated by *C. hortensis*. More southerly only few isolated populations were found, in Tachov (western Bohemia), Tuchlovice, Unhošť and Zásmyky (central Bohemia) and Chotusice, Havlíčkův Brod and Dolní Krupá (eastern Bohemia). The latter localities should be added to the list published by Honěk (1995).

*C. vindobonensis* was distributed at lowland localities of central Bohemia, along the Labe river and its major tributaries, Jizera, Vltava and Ohře, and in the Středočeský kras karst area of central Bohemia. Several occasionally recorded localities are shown in Fig. 2.



Fig. 3 Geographic distribution of *C. nemoralis* populations with high proportions of colour and shell banding forms. The large points represent populations with (A) >80% of pink individuals, (B) >90 % of 12345 individuals, (C) >30 % of 00000 individuals, (D) >50 % of 00300 individuals, and (E) >5 % of 00345 individuals. The small points represent other localities where >10 individuals of *C. nemoralis* were collected.

### 3. Frequency of shell colour and banding forms in local populations

Bohemian populations of *C. vindobonensis* are practically monomorphic. The only variation is a reduction of the bands 1 and 2, and occurrence of hyalozonate individuals (Ložek 1956). Only few individuals showing this type of variation were found. The variation of *C. nemoralis* and *C. hortensis* is discussed below.

#### 3.1 Shell colour

Both *C. hortensis* and *C. nemoralis* have either a yellow or a pink shell colour. The populations with an increased percentage of the pink form were more frequent in *C. nemoralis* than *C. hortensis* (Fig. 1). In *C. nemoralis* there was no trend to local aggregation of populations with a high frequency of the pink morph (Fig. 3). In fact, the range of variation in the frequency of pink form was similar in 53 populations collected on a small area of the towns of Litoměřice and Nový Bydžov (ca 20 km<sup>2</sup>), and the 125 populations from the rest of the country. *C. hortensis* populations with a high frequency of pink form were also scattered over the whole country (Fig. 4) and interspersed with populations containing small percentage of pink individuals.

#### 3.2 Shell banding

Populations of *C. hortensis* consisted of bandless 00000 or five banded 12345 individuals. In local populations the morphs were present in proportions ranging from 0 to 100 %. Populations consisting of >90 % unbanded individuals were aggregated in the eastern part of the country (Fig. 4) while populations consisting only of 12345 individuals were found more frequently in the west (Fig. 4). However, these populations were interspersed with populations containing intermediate proportions of both forms. Many *C. hortensis* populations contained banded individuals with two or more confluent bands. The distribution of populations with a high frequency of individuals with fused bands was mosaic.

Populations of *C. nemoralis* contained shell banding morphs 00000, 00300, 00345, and 12345 whose distribution was discussed in detail by Honěk (1995). The populations with a high percentage of morphs 00000 and 12345 (Fig. 3) were scattered over the whole area of species' geographic distribution while the ones with a high frequency of 00345 and 00300 morphs were aggregated (Fig. 3). The distribution of the latter morphs may be considered as an example of area effects. The populations with high proportions of individuals with band fusions were scattered evenly over the whole territory.

### 4. Morph frequency and the altitude of the locality

We investigated the relationship between the above sea level altitude of the locality (which is a correlate of climatic conditions) and proportion of morphs which might have a thermoregulatory function. There was no correlation between the altitude of the locality and the percentage of pink individuals, or the percentage of pooled melanic (123)(45) and (12345) morphs in the respective populations.

#### DISCUSSION

In Western Europe, the intraspecific variation of shell colour and banding patterns in *Cepaea* species was studied by many authors, since the late 19th century. The materials were sampled at

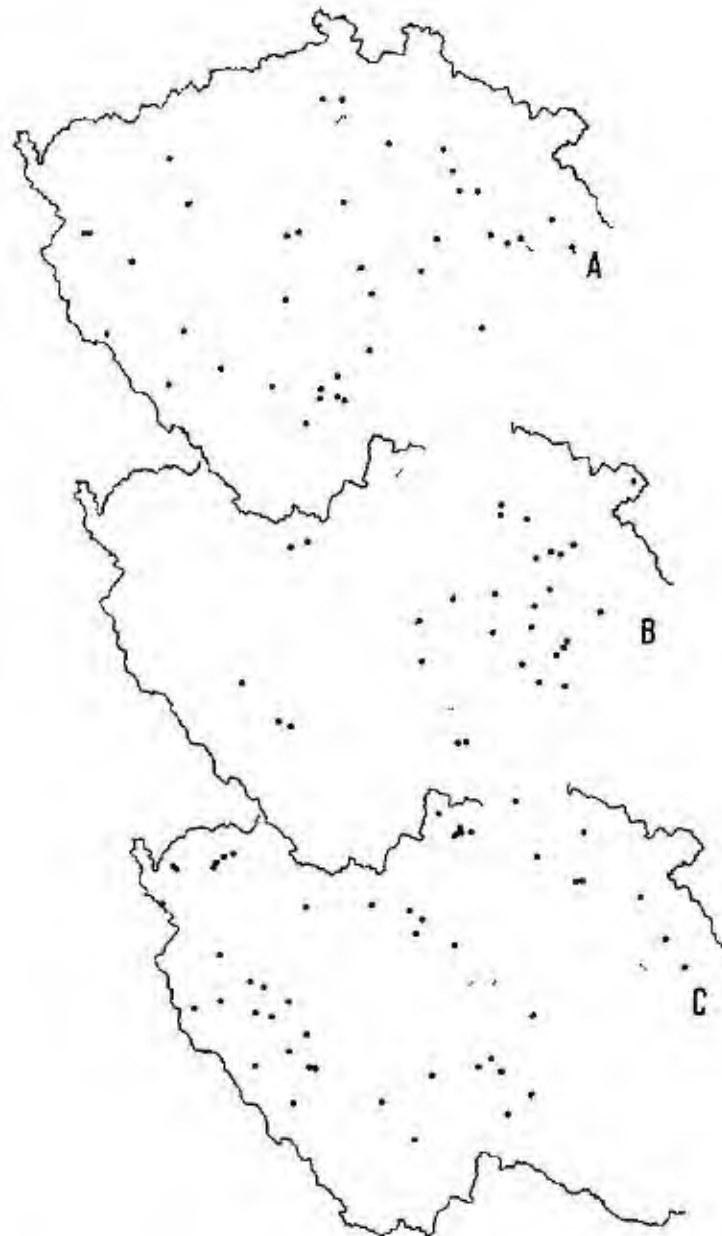


Fig. 4 Geographic distribution of *C. hortensis* populations with high proportions of colour and shell banding morphs. The large points represent populations with (A) >20% of pink individuals, (B) >90 % of 00000 individuals and (C) 100% of 12345 individuals. The small points represent other localities where >20 individuals of *C. hortensis* were collected.

a vast number of localities, particularly in Britain, Spain, France and Germany. The local variation in morph frequency was related to climatic and microclimatic factors (Jones & Irving 1975, Ramos 1984, 1985, Ratel et al. 1989, Khemici et al. 1989), visual selection by avian predators (Cain & Sheppard 1954, Cain 1968) and historical events including founder effects (e.g. Lamotte et al. 1988) which modify the action of selective forces. Despite the large body of accumulated knowledge the problem resisted the conclusive solution (Jones 1973a, Jones et al. 1977, Cain 1983, Lamotte 1988). Comparative studies of morph frequencies in local populations continue in contributing relevant information for the study of *Cepaea* polymorphism. This study presents results from Bohemia, a territory rather isolated by surrounding mountains and spatially separated from Western Europe, with continental climatic conditions.

There exist several analogies as well as important differences between Bohemian and West-European populations of *C. nemoralis* and *C. hortensis*.

(1) The geographic area of *C. nemoralis* distribution is smaller than the one of *C. hortensis* (cf. Ložek 1956, Jones & Clarke 1969, Ramos 1985). In the centre of the overlap of geographic areas of both species, the oceanic area of Western Europe, both species occupy similar urban and country habitats and frequently occur in mixed populations (Schulder & Schulder 1953, Mazon et al. 1989). Habitat preferences of both species in Bohemia are different. *C. nemoralis* occupies urban sites. *C. hortensis* lives in the country habitats as well as at urban sites. The latter are occupied by *C. hortensis* in absence of *C. nemoralis*. Otherwise *C. nemoralis* replaces *C. hortensis* at urban sites almost completely and both species rarely occur in mixed populations (Honěk 1995). Similar differentiation of habitat preferences was observed also in Poland (Rafinski 1981). Our results indicate also different altitudinal preferences. *C. hortensis* occupied many localities at altitudes of >300 m a.s.l. where *C. nemoralis* populations were less frequent. However, this "tolerance" to highland conditions could be a consequence of the limited geographic distribution of *C. nemoralis*. *C. hortensis* inhabits highland areas of Českomoravská vrchovina and submontane areas of western and southern Bohemia where *C. nemoralis* is absent. Climatic differences between lowland and highland areas are small, not likely to limit the presence of *C. nemoralis* although this species is probably less tolerant to harsh conditions than *C. hortensis* (cf. Jones & Clarke 1969).

(2) *Cepaea hortensis* and *C. nemoralis* differ in overall proportion of shell colour morphs. The average proportions are in accordance with continental trends. In *C. nemoralis* the average frequency of pink morph is in between the Mediterranean populations with a high frequency of yellow morph and Atlantic populations with increased frequency of pink form (Lamotte 1988). The overall proportions in Bohemian populations may be affected by continental climate with average temperatures lower than in the Mediterranean region and scarce rainfalls. Local effects of climatic selection (Jones & Irving 1975, Ramos 1984, Lamotte et al. 1988, Khemici et al. 1989) could not be detected. The average frequency of pink form in *C. hortensis* populations is lower than in *C. nemoralis*. This situation is similar to Western Europe, France (Guerrucci 1974), Britain (Cain et al. 1969) and Germany (Schulder & Schulder 1953).

(3) Differences were found also in occurrence of shell banding morphs. Common morphs of *C. nemoralis* present in Western Europe, 00000, 00300, 00345, and 12345 were found also in Bohemia. By contrast, only two morphs of *C. hortensis*, 00000 and 12345, occur in Bohemia, in contrast to French populations where also 00300, 10305, and 00345 morphs were found (Guerrucci 1974). Similar constraints on variation, however, were found in British (Cain et al. 1969) and German (Schulder & Schulder 1953) populations of *C. hortensis*.

(4) Patterus of variation between local populations of *Cepaea* in Bohemia and Western Europe are similar in that frequencies of shell colour and banding morphs vary largely between populations separated by a small distance or even across a population continuum (Wolda 1969). As a result, the distribution of populations with different frequencies of particular morphs is

usually mosaic. Area effects, occurrence of a high proportion of a morph in several populations aggregated in an ecologically heterogeneous area, were established in West European populations of *C. nemoralis* (Cain & Currey 1963). It was suggested that their existence is associated with unstable habitats and their origin favoured by "historical" events (founder effect) rather than by the selection process (Cameron et al. 1984, Cameron & Dillon 1984). The existence of area effects in Bohemian populations of *C. nemoralis* is an interesting exception. The localities with a high frequency of 00300 and 00045 morph are aggregated on a rather large area. I suppose that the area effects are a consequence of the founder effect during the recent expansion of this species in northern Bohemia (Honěk 1995). In contrast to *C. nemoralis*, no trace of area effects was found in *C. hortensis* whose populations are long established in this area.

In this work only a marginal interest was paid to *C. vindobonensis*. It is a pontic species which inhabits south-eastern and eastern-central Europe. Czech Republic is near the north-west edge of its geographic distribution (Ložek 1956). The absence of variation in many Bohemian populations contrasts with southern populations where hyalozonate individuals may be rather frequent (Jones 1973a, 1974). The difference is probably due to lower intensity of thermal stress in Bohemian populations.

Compared with earlier results (Ložek 1956), our data confirmed the statements on habitat preferences of the *Cepaea* species, and indicated the spreading of the area of geographic distribution of *C. nemoralis* (Honěk 1995). Curious is the present absence of this species at the territory of Prague (Juřčková 1994). This is a cross-road of traffic and offers many sites convenient for *C. nemoralis*.

#### Acknowledgement

I thank Dr Vojen Ložek for helpful comments during preparation of the manuscript.

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## APPENDICES 1 AND 2

The frequency of shell colour and banding morphs in local populations of *C. hortensis* and *C. nemoralis*. GN - geographic position of the locality indicated by the number of square in the reference grid used for faunistic mapping of the Czech Republic (see Material and Methods).

		Appendix 1: <i>Cepaea hortensis</i>															
		FREQUENCY OF COLOUR AND SHELL BANDING MORPHS															
GN	Locality	YELLOW								PINK							
		00000	12345	12345	12345	12345	12345	12345	12345	00000	12345	12345	12345	12345	12345	12345	12345
5250	Hard Pansy	21								21							21
5251	Kriva's	27								27							27
5252	Kriva's	4	8							12	9	5					26
5253	Zahradky	30	4							34	12						46
5254	Quadrant	52	10							62	1	1					64
5257	Yellow Band	1	15							16	4						20
5257	Yellow Band	19								19	1						20
5259	Interline	85								85							85
5452	Interline	8	18							26							34
5453	Panacea	35	1	2	4					42	9						51
5455	Zachin	50	42	8						100							142
5455	Duba	131	25							156	8	1	1				166
5455	Barling	1	31	7	1					40							40
5456	Vrchovany	28								28							28
5456	Chum	32	7	11						50							60
5456	Dobry	28								28							28
5456	Kriva's	16								16							16
5457	Rozsudek pod Travnici	24	23	6	2					55	5						60
5458	Grass	58	7							65							65
5500	Kosmonov	8	2							10	12	1					23
5507	Slavka	12	1	3	1	1	1	1	1	20							24
5508	John	1	10	1	3	2	1	1	1	20							24
5508	John	87	39	1	21	5				153	3						156
5508	John	20	2							22							22
5508	John	28	11	1	2					42							42
5508	Nová Paka	78	14	4	3	1	2	4	1	106	4	3					113
5509	Laví Bělá	40	77	8	10	6	3	5		189							189
5509	Laví Bělá	20	21	3	5	4	1	1	5	61							61
5509	Marin	12	51	11	1	2				77							77
5509	Marin	1	18	2	4	2				23							23
5509	Nová Paka	17	64	3	4					88							88
5509	Nová Paka	6	18							24							24
5509	Chalovka	3	37	2						42							42
5509	Hozdín	31								31							31
5509	Pendle	7	15							22							22
5509	Chalovka	4	18	5	5	2	1	4	5	39	11						50
5509	Kopce	11	2	3	4	1	1		8	29							29
5509	Nová Paka	18	4							22							22
5509	Nová Paka	26	11	4					1	42	18	5	2				63
5509	Chalovka	18	2	2	1	6	2	9	2	38							38
5509	Chalovka	3	13	2	5	1	1	1	7	24							24
5509	Vojs	9	29	7	34	1	14	1	3	108							108
5509	Chalovka	91	48	2						141							141
5509	Chalovka	20								20							20
5509	Chalovka	23	2	1	2				1	27							27
5509	Laví Bělá	10	7							17	3						20
5509	Nová Paka	13	8							21							21
5509	Kopce	31	2	2	1					36							36
5509	Chalovka	40	1							41							41
5509	Božany	50								50							50
5509	Chalovka	23								23							23
5509	Karlov Vary	3	30							33							33
5509	Karlov Vary	8	48							56	1	2					61
5509	Karlov Vary	100								100	15						115
5509	Karlov Vary	2	23							25	1						26
5509	Karlov Vary	18	20							38	3	2					43
5509	Matkov	10	1	1						12	16						28
5509	Matkov	21	8							29							29
5509	Matkov	10	12							22							22
5509	Chalovka	2	12	9	2	1	14	2	3	30							30
5509	Nová Paka	7	5	2						14							14
5509	Nová Paka	34	2							36	14	4					44
5509	Matkov	22	8	1						31	13	1	1	2	1	4	43
5509	Matkov	2	22							24	13						37
5509	Matkov	112	5	2						119							119
5509	Matkov	26	6	18						50							50
5509	Matkov	48	23							71							71
5509	Matkov	59	5							64							64
5509	Matkov	37								37							37
5509	Matkov	138	1							139							139
5509	Matkov	32								32	5						37
5509	Matkov	26	2							28							28
5509	Matkov	36	7							43							43
5509	Matkov	18								18							18
5509	Matkov	36								36							36
5509	Matkov	88								88							88
5509	Matkov	17								17	18						35
5509	Matkov	27								27							27
5509	Matkov	21	1							22							22





Appendix 2: *Cepaea nemoralis*

FREQUENCY OF COLOUR AND SHELL BANDING MORPHS

[illegible]







Contribution to the taxonomy of Mordellidae from South and East Africa  
(Coleoptera: Mordellidae). Part 1.

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Received January 6, 1995, accepted February 9, 1995

Published June 22, 1995

Taxonomy, new species, new combination, keys, Coleoptera, Mordellidae, Afrotropical region.

**Abstract.** *Mordellaria binotata* sp. n., *Glipostenoda ferruginea* sp. n., *G. nigricornis* sp. n., *G. exellens* sp. n. and *Neomordellistena* (s. str.) *rueri* sp. n. are described. New combination *Stenomorda disparilis* (Champion, 1917) from *Mordella* Linnaeus 1758 is proposed.

The present paper is based on the material of Mordellidae collected by J. Klapperich in the Republic of South Africa in 1981 and deposited in the Natural History Museum "A. Koenig", Bonn. Some duplicates are deposited in author's collection. The paper represents a complement of previous papers by Franciscolo (1965, 1967). Genera *Mordellistena* Costa, 1854 and *Mordellina* Schilsky, 1908 will be treated in the second part, which will be published later.

*Stenomorda disparilis* (Champion, 1917) **comb. n.**

*Mordella disparilis* Champion, 1917: 180

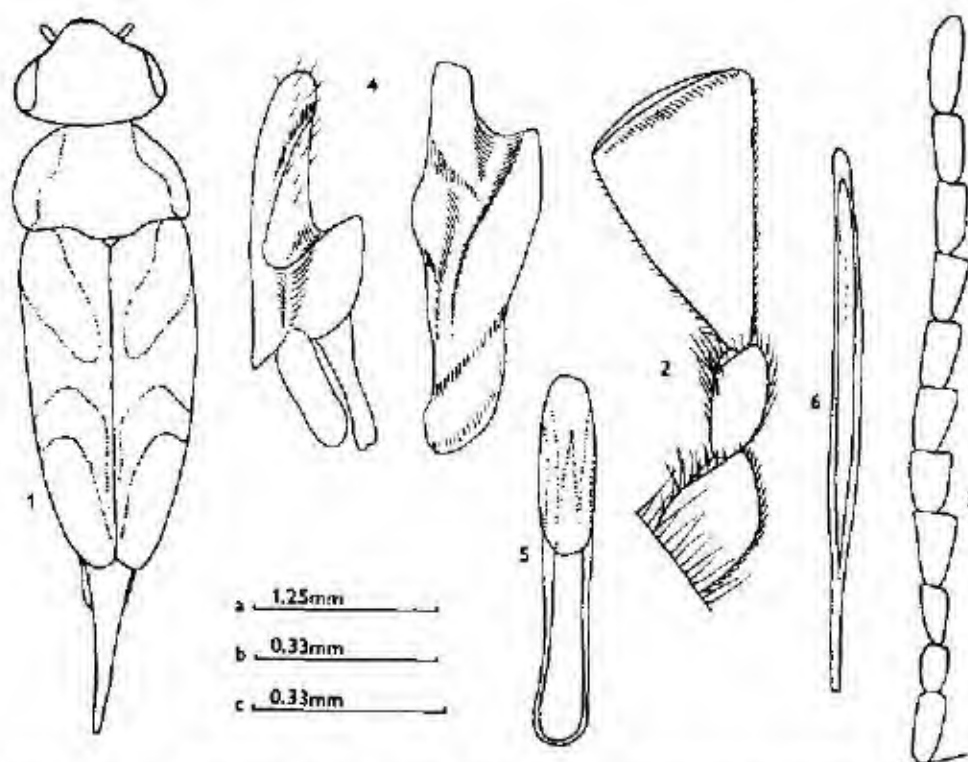
The equal size of the fourth and fifth antennal segments (the fourth segment being distinctly longer and wider than the third one, fig. 3) classify this species as a member of the group of genera *Binaghtia* (Franciscolo, 1965). Distinctly developed dorsal ridge of posterior tibia and intermediate tarsus shorter than mesotibia suggest its appurtenance to the genus *Stenomorda* Ermisch, 1950. *Stenomorda disparilis* is closely related to *S. motoensis* (Pic, 1931) and *S. vittatipennis* (Pic, 1931) from Congo. It shares with a completely yellow-red head, but it differs from them at the first sight by the black ventral surface and different colour pattern of elytra (Ermisch, 1968). The species with adjacent areal, *S. fairmairei* (Pic) from Madagascar, has a completely black head. For the shape of body, maxillary palpus, antenna and male genitalia see Figs 1-6.

Length including pygidium 5.0 - 5.2 mm.

**MATERIAL EXAMINED.** 2 males, Seychelen, Mahe, Cascade, 14.10.1991, Mandl leg. (1 male deposited in my collection). 1 male, Seychelen, Mahe, Le Nioi, 28.10.1991, Mandl leg., deposited in Naturhistorisches Museum, Wien.

*Mordellaria binotata* sp. n.

Body short, rounded and rather convex (Fig. 7). Colour black, only anteclypeus, anterior margin of labrum, maxillary palpi, six proximal segments of antennae, fore legs and transverse humeral band of elytra (reaching posteriorly to about two thirds of the length of elytra) yellow-brown. Intermediate femora and tibiae dark brown. Pubescence grey-black, becoming darker



Figs 1-6. *Stenomorda disparis* (Champion), male, Seychelles Isl. 1 - general view, 2 - maxillary palpus, 3 - antenna, 4 - left and right paramere, 5 - phallobasis; 6 - penis. Scale a - 1, b - 3, 4, 5, c - 2, 4.

posteriorly. Three spots of darker hairs are developed on pronotum, the yellow-brown spots of elytra are covered with golden-yellow hairs. Pubescence of ventral surface golden-brown, only on posterior borders of abdominal sternites and the apex of pygidium grey-black.

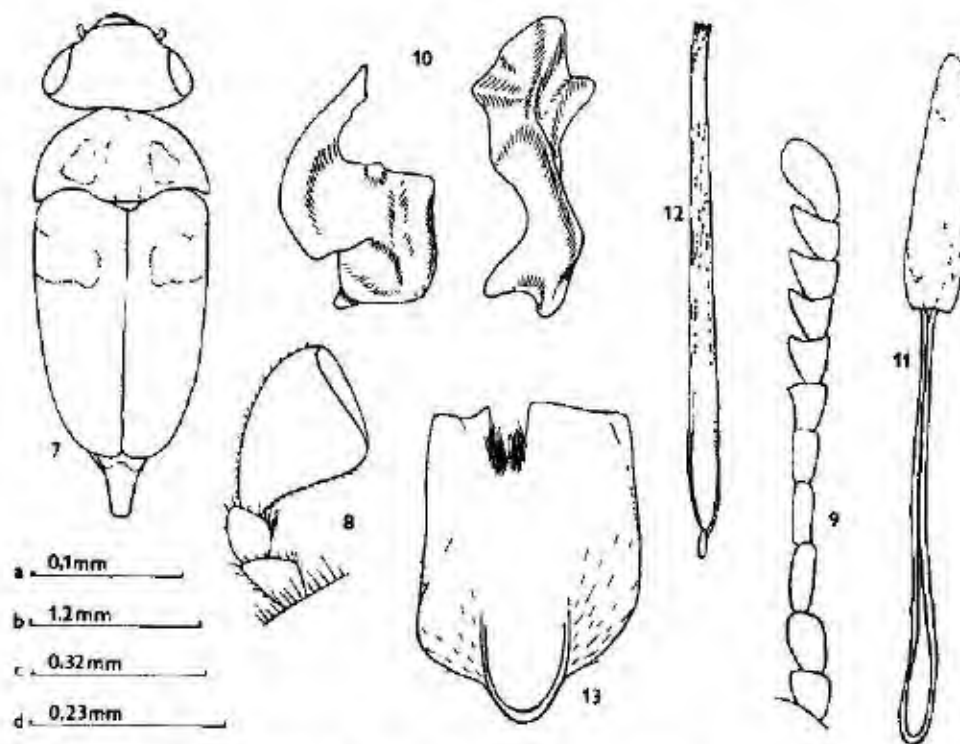
Head very broad (maximum length to maximum width ratio as 4.6 : 6.7), distinctly narrower than pronotum, gently emarginate posteriorly. Eyes comparatively large, very broadly oval, finely faceted, quite glabrous. Temples absent. Punctuation of head very fine and dense. Antenna and maxillary palpus as figured (Figs 8, 9).

Pronotum strongly transverse (width to length ratio as 8 : 5), widest at the basal third, semicircular, without a collar-shaped prolongation of anterior portion; posterior lobe rather flatly arcuate, broad. Sides (lateral view) straight, posterior angles moderately obtuse and strongly rounded. Scutellum broadly triangular, with silvery pubescence.

Elytra short (hardly more than 1.5 times longer than their combined width), strongly convex, only moderately tapering posteriorly behind humera, separately rounded at the apex.

Pygidium short, broad, only by one third longer than hypopygium.

Anterior tibia gently curved inwards, without longer outstanding hairs. Anterior tarsus a little shorter than tibia, its first segment twice as long as the second one, particular segments becoming gradually shorter; penultimate segment minute, longer than wide, truncate. Intermediate tibia shorter than tarsus. Posterior tibia, besides a short apical ridge, with one distinct dorsal ridge. The first segment of posterior tarsus with one distinct dorsal ridge, following segments simple. Termi-



Figs 7-13 *Mordellaria binotata* sp. n., male, holotype. 7 - general view, 8 - maxillary palpus, 9 - antenna, 10 - left and right paramere, 11 - phallobasis, 12 - penis, 13 - 8-th internal sternite. Scale: a - 0.1 mm, b - 1.2 mm, c - 0.32 mm, d - 0.23 mm.

nal spurs of metatibia black-brown, outer one reaching less than one fifth of the length of the inner one.

Male genitalia as figured (Figs 10-12). The eighth urosternite almost quadrate, its distal margin truncate laterally, emarginate in the middle and within the emargination covered with dense black hairs (Fig. 13).

Length from the tips of mandibles to the tips of elytra 3.2 mm, to the apex of pygidium 3.7 mm.

NAME DERIVATION. Named after its very distinct two humeral bands.

DIFFERENTIAL DIAGNOSIS. The fourth known species of *Mordellaria* Ermisch, 1950 from South Africa may be distinguished from the other species according to the following key (according to Franciscolo, 1965):

- 1(2) Segments of posterior tarsi without ridges. Length 3.2 mm. East of the Cape Province. *M. pulchella* Ermisch, 1954.
- 2(1) Basal segment of posterior tarsus with distinct dorsal ridge. Ridge sometimes developed also on the second segment. *M. hessei* Franciscolo, 1965.
- 3(4) Antennae thin, filiform, segments 5 to 10 hardly wider than the four basal segments, each of them much longer than broad. Eyes sparsely pubescent. Length 4 mm. Zululand.
- 4(3) Antennae robust, short, strongly dilated beginning from the fifth segment. Each of the segments 5 to 10 wider than long, strongly serrate. Eyes glabrous.

- 5(6) Second segment of posterior tarsus without dorsal ridge. Elytra very short (male), only a little more than 1.5 times longer than their combined width. Body black, except for transverse yellow-brown band covered with brightly golden-yellow hairs and reaching from humera to about two thirds of the length of elytra. Rest of the dorsal surface with grey-black pubescence. Length 3.7 mm. Natal ..... *M. binotata* sp. n.
- 6(5) Second segment of posterior tarsus with short and distinct dorsal ridge. Elytra twice as long as their combined width (female), besides yellow-red semicircular humeral spot bearing also transverse band in the apical third. The light spots on elytra covered with golden pubescence, which moreover makes up another transverse band situated between the two light spots, just behind the midlength of elytra. Length 4.3 mm. Cape Province, Natal ..... *M. africana* Franciscolo, 1956

TYPE MATERIAL. Holotypus, male, SWA, Natal prov., St. Lucia, 10m, 25-27.10.1981, J. Klapperich leg.; deposited in the Naturhistorisches Museum "A. Koenig", Bonn

### *Glipostenoda ferruginea* sp. n.

Body short, strongly rounded and strongly convex (Fig. 14), entirely yellow-brown with golden-yellow pubescence.

Head flatly convex, wider than long (width to length as 5.3 : 4.2). Eyes comparatively small, finely faceted and pubescent. Temples not developed (Fig. 17). Second segment of maxillary palpus as wide as the third one, terminal segment narrowly securiform, its inner angle shifted somewhat behind the midlength of the segment (Fig. 15). Antennae rather long, the fourth segment distinctly longer and slightly wider than the third one; the fifth segment by one third longer and by one fourth wider than the fourth one; each of the segments 5 to 10 is 1.8 times longer than wide; terminal segment oblong oval, 2.3 times longer than wide (Fig. 16).

Pronotum wider than long (width to length as 6.7 : 5.8). Anterior portion arcuately elongate, without a collar-shaped prolongation. Sides (lateral view) gently incurved, posterior angles almost rectangular, rounded.

Scutellum small, triangular, with rounded apex.

Elytra strongly convex, twice as long as their combined width, at sides rounded, almost simultaneously rounded at the apex, finely and sparsely punctate, shining.

Pygidium elongate, conical, 2.3 times longer than hypopygium.

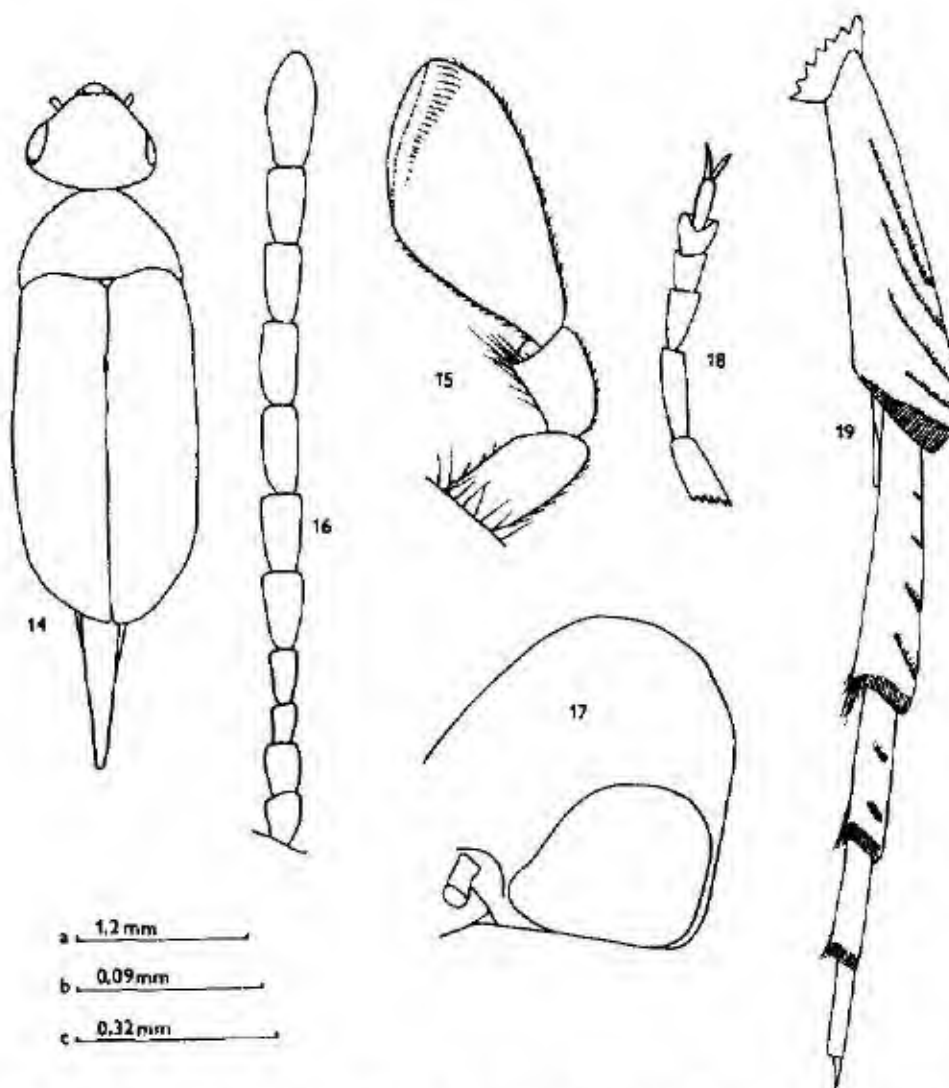
The first segment of anterior tarsus twice as long as the second one; second segment by one third longer than the third one; the fourth segment wider than long and by third shorter than the third one, deeply bilobed and wider than the preceding one; terminal (fifth) segment almost twice as long as the fourth one (Fig. 18). Intermediate tarsus as long as tibia. Metatibia, besides apical ridge, with three long and very oblique lateral ridges, the proximal one being fine. First segment of posterior tarsus with four, second segment with two ridges (Fig. 19). Outer apical spur of metatibia reaching approximately one half of the length of the inner one.

Length from tips of mandibles to tips of elytra 3.7 mm, to the tip of pygidium 4.7 mm.

NAME DERIVATION. Named after its entirely yellow-brown coloured body.

DIFFERENTIAL DIAGNOSIS. *G. ferruginea* sp. n. maybe incorporated into the key to afrotropical species by Franciscolo (1967) as follows:

- 9(10) Metatibia with two very oblique, but comparatively short, lateral ridges. The first and second segments of posterior tarsus bearing three (very oblique) and two (short and oblique) ridges respectively. Body red-yellow, elytra as well as the disc of pronotum with elongate black spot, missing in some specimens from Natal and Transvaal. Length (including pygidium) 4.5 mm. "Caffraria", Natal, Transvaal ..... *G. pulla* (Fahraeus, 1870)
- 10(9) Metatibia with three strong and oblique lateral ridges, the proximal ridge being extremely oblique and markedly finer than following ones, which are very strong and different. The first and second segment of posterior tarsus bearing four and two ridges respectively.



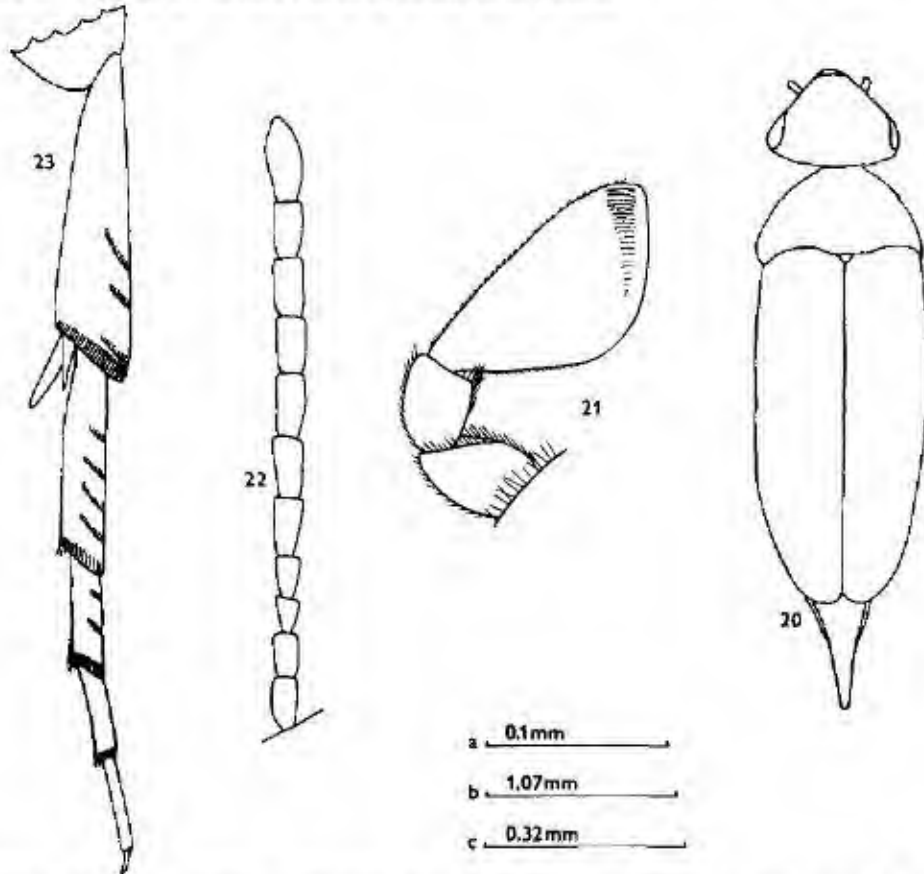
Figs 14-19 *Ghynstenoda ferruginea* sp. n., female, holotype: 14 - general view; 15 - maxillary palpus; 16 - antenna; 17 - eye; 18 - anterior tarsus, 19 - posterior tibia and tarsus. Scale: a - 14, b - 15, c - 16, 17, 18, 19

- a(b) Completely yellow-brown. Elytra less than twice as long as their combined width, laterally rounded. Pygidium twice as long as hypopygium. Length (including pygidium) 4.7 mm. Transvaal ..... *G. ferruginea* sp. n.  
b(a) Rusty with black head. Elytra 2.3 times longer than their combined width, rather parallel-sided. Pygidium only 1.5 times longer than hypopygium. Length (including pygidium) 5.7 mm. Congo ..... *G. desaegei* Ermisch, 1952

TYPE MATERIAL. Holotypus, female, SA, Prov. Transvaal, Blydepoort, 20.11.1981, J. Klappenach leg.; deposited in the Naturhistorisches Museum "A. Koenig", Bonn.

*Glipostenoda nigricolor* sp. n.

Body comparatively short, moderately rounded and convex (Fig. 20). Completely black except for red-brown palpi, antennae, anterior legs and intermediate tibiae and tarsi. Intermediate femora and entire posterior legs black-brown. Terminal spurs of metatibia yellow. Pubescence black-brown, only on humera and along suture paler, golden.



Figs 20-23. *Glipostenoda nigricolor* sp. n., female, holotype. 20 - general view; 21 - maxillary palpus; 22 - antenna; 23 - posterior tibia and tarsus. Scale: a - 21, b - 20; c - 22, 23.

Head flatly convex, wider than long (as 4.3 : 3.5). Eyes small, somewhat coarsely faceted, pubescent. Tempora not developed. Second segment of maxillary palpus slightly wider than the third one, terminal segment shortly and broadly securiform, its inner angle situated somewhat behind midlength of the segment (Fig. 21). Antennae rather short, segment 3 shorter than 4, each of the segments 5 - 10 about 1.5 times longer than wide (Fig. 22).

Pronotum wider than long (as 5.4 : 4.2), its anterior portion semicircular without a collar-like prolongation. Sides in lateral view straight, posterior angles broadly obtusely rounded.

Scutellum small, with broadly rounded apex.

Elytra flatly convex, 2.4 times longer than their combined width, indistinctly separately rounded



at the apex, shining, with fine rasp-like puncturation.

Pygidium conical, twice as long as hypopygium.

Penultimate segments of anterior and intermediate tarsi bilobed, quadrate and wider than the preceding segments; first segment by one third longer than the second one, that almost twice as long as the third segment, which is but slightly longer and narrower than the fourth one; terminal segment by one half longer than the penultimate one. Intermediate tarsus as long as mesotibia. Metatibia, besides the apical ridge, with two very short and only slightly oblique lateral ridges. The first and second segments of posterior tarsus with four and two ridges respectively (Fig. 23). Outer terminal spur of metatibia reaching one third of the length of the inner one.

Length from tips of mandibles to tips of elytra 3.0 mm, to tip of pygidium 3.7 mm.

NAME DERIVATION. Named after its entirely black coloured body.

Position of *G. nigricolor* sp. n. in the key to the South African species by Franciscolo (1967):

- 12(3) Posterior tibia with 2-4 short and little oblique lateral ridges, which are parallel to the posterior margin of tibia  
a(d) Only first and second segments of posterior tarsus with ridges  
b(c) Body completely black (except mouth parts, palpi, antennae, anterior legs and intermediate tibiae and tarsi). Terminal segment of maxillary palpus short and broadly securiform, its inner angle situated somewhat behind midlength of the segment. Metatibia with two very short and only slightly oblique lateral ridges. Antennae short, their fifth segment 1.5 times longer than wide. Length (including pygidium) 3.7 mm. S.W Africa ..... *G. nigricolor* sp. n.  
c(b) Black, partly somewhat brownish, with red-brown pattern of elytra consisting of humeral spot, transverse band behind the midlength of elytra and common apical spot. Terminal segment of maxillary palpus elongate and narrowly securiform, its inner angle situated in the distal fourth of the segment. Metatibia with three short lateral ridges (the upper one somewhat rudimentary). Length (including pygidium) 4.2 mm. S.W Africa ..... *G. excellens* sp. n.  
d(a) Ridges developed on three basal segments of posterior tarsus  
13(14) Continued according to Franciscolo (1967).

TYPE MATERIAL. Holotypus, female, SWA, Tsitsikamma Berge, Stormsriver, 1.12.1981, J. Klapperich leg.; deposited in the Naturhistorisches Museum "A. Koenig", Bonn.

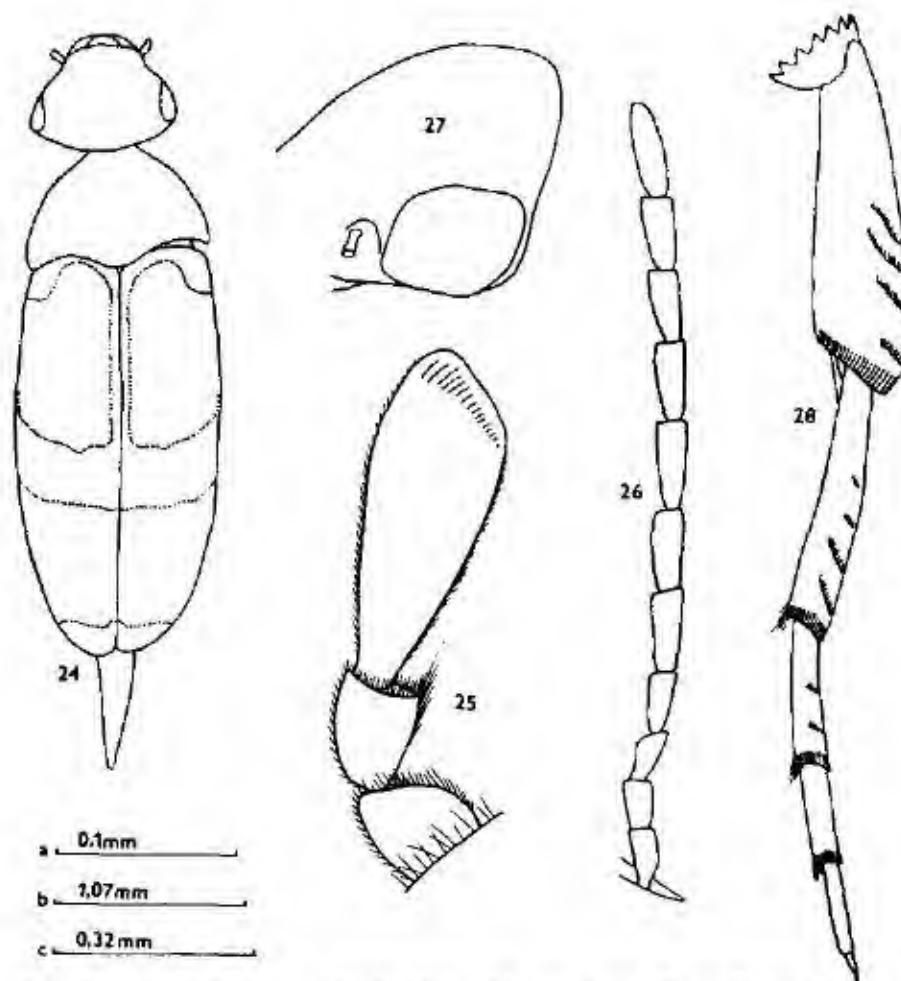
#### *Glipostenoda excellens* sp. n.

Body short, rounded and convex (Fig. 24). Colour black-brown to black, elytra with red-brown pattern consisting of elongate humeral spot, narrowly connected along suture with transverse band behind the midlength of elytra and also of apical portion of elytra. Anterior portion of the head paler, anteclypeus yellow, labrum brown, mandibles (excluding tips) and maxillary palpi red-brown. Antennae brown and gradually infusate posteriorly, their terminal segment being quite black. Anterior and intermediate legs brown, intermediate femora and posterior legs dark brown. Terminal spurs of metatibia yellow-red. Ventral surface black, anterior portion of metasternum red-brown. Pubescence of dorsal surface black-brown, on elytral pattern brightly golden-yellow.

Head rather flatly convex, width to length ratio as 5 : 4. Eyes comparatively small, finely faceted and pubescent. Temples absent (Fig. 27). Second and third segment of maxillary palpus almost equally broad, terminal segment elongate and narrowly securiform, its inner angle situated in the distal fourth of the segment (Fig. 25). Antennae long, the third segment shorter than the fourth one, each of the segments 5-10 more than twice as long as wide (Fig. 26).

Pronotum wider than long (width to length ratio as 6 : 5), without collar-shaped anterior projection. Sides (lateral view) almost straight, posterior angles obtusely rounded.

Scutellum triangular, small and narrow.



Figs 24-28. *Glipostenoda excellens* sp. n., female, holotype: 24 - general view; 25 - maxillary palpus; 26 - antenna; 27 - eye; 28 - posterior tibia and tarsus. Scale: a - 25; b - 24; c - 26, 27, 28.

Elytra convex, 2.2 times longer than their combined width, indistinctly separately rounded at the apex, shining, with very fine rasp-like puncturation.

Pygidium slender, conical, 2.3 times longer than hypopygium.

The first segment of anterior tarsus by two thirds longer than the second one, that a little more than twice as long as wide; third segment by 1.5 times longer than wide, by one third shorter than the second one and by one third longer than the fourth segment; the fourth segment quadrate, bilobed and somewhat wider than the preceding ones; terminal segment only 1.5 times longer than the fourth one. Intermediate tarsus as long as tibia. Metatibia, besides the apical ridge, with three short lateral (proximal one somewhat rudimentary), which are parallel to the apical margin of tibia. The first segment of posterior tarsus with four ridges (two proximal ones very rudimentary), the second segment with two little distinct ridges, following segments smooth (Fig. 28). Outer terminal spur of metatibia reaching three fifths of the length of the inner one.

Length from tips of mandibles to tips of elytra 3.5 mm, to the tip of pygidium 4.2 mm.

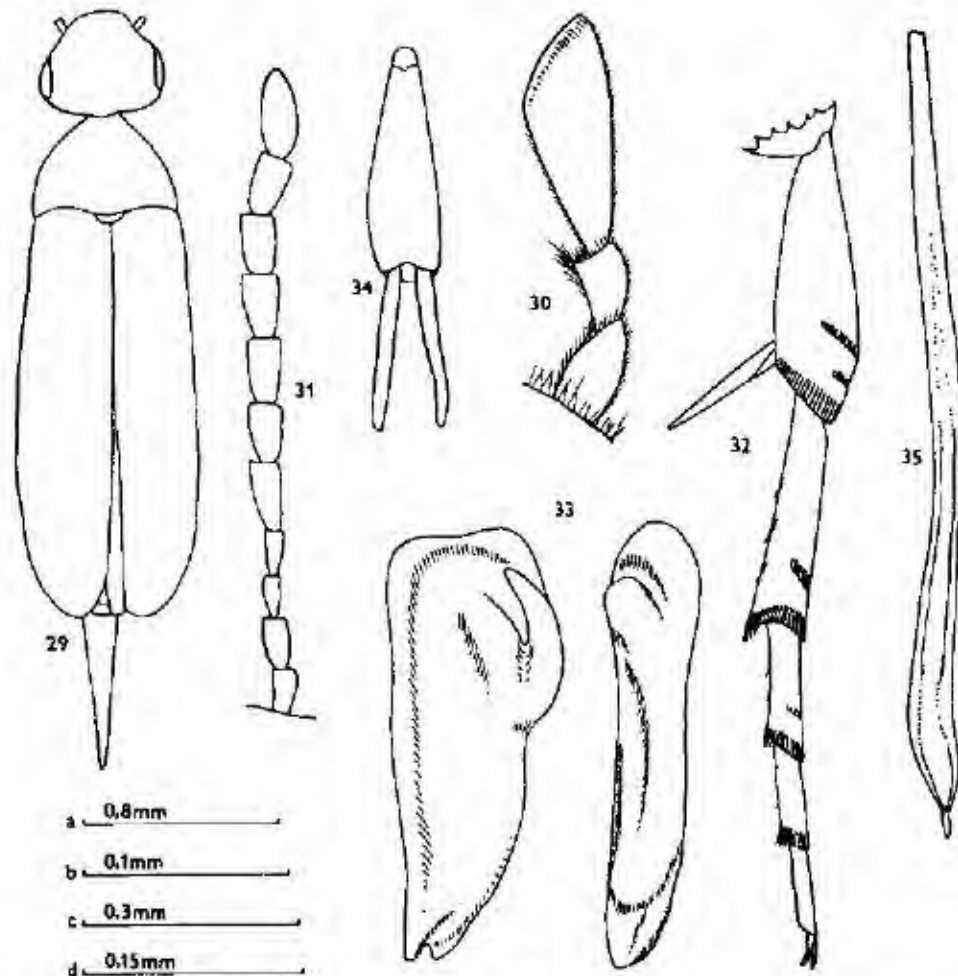
NAME DERIVATION. Named after its delicious coloured elytra.

DIFFERENTIAL DIAGNOSIS. For diagnostic character see the key by *Glipostenoda nigricolor* sp. n.

TYPE MATERIAL. Holotypus, female, SWA, Tsitsikamma Berge, Stormsriver, 1.12 1981, J. Klappenich leg.; deposited in the Natural History Museum "A. Koenig", Bonn.

*Neomordellistena* (s. str.) *roeri* sp. n.

Body slender, parallel-sided and strongly convex (Fig. 28). Yellow with golden-yellow pubes-



Figs 29-35 *Neomordellistena roeri* sp. n., male, holotype: 29 - general view, 30 - maxillary palpus; 31 - antenna; 32 - posterior tibia and tarsus, 33 - paramere; 34 - phallobasis; 35 - penis. Scale: a - 29, b - 30, c - 31, 32, 34, 35, d - 33.

cence, only antennae from the fifth segment, as well as three basal abdominal segments, brown. Apical marking of all segments of posterior legs as well as all ridges black.

Head strongly convex, slightly wider than long (as 5 : 4.5). Eyes oblong oval, finely faceted and pubescent. Neither temples or temporal angle developed. Second segment of maxillary palpus slightly wider than the third one, terminal segment in male narrowly securiform with inner angle situated within its distal fourth (Fig. 29). Antennae (Fig. 30) rather long, filiform, the first and second segments subequal, third segment minute and elongate, by almost one half narrower and shorter than the second one; the fourth segment as wide as, but slightly longer than the third one; the fifth segment by about one fourth longer and wider than the fourth one, almost twice as long as wide; following segments gradually slightly abbreviated, terminal segment oblong oval, twice as long as wide and by nearly one fourth longer than the penultimate one; antennae in female shorter, the fifth segment nearly 1.5 times longer than wide.

Pronotum wider than long (as 10.5 : 9), its anterior margin with collar-shaped prolongation. Sides (lateral view) emarginate, posterior angles rectangular.

Scutellum very broadly semicircular, with short apical point.

Elytra 2.8 times longer than their combined width, parallel-sided, with very fine rasp-like puncturation and sparse golden-yellow pubescence.

Pygidium very slender, conical, three times as long as hypopygium.

Anterior tibia in male straight, feebly swollen, without longer hairs on its inner side. All segments of anterior tarsus but the terminal one equally broad, the fourth segment quadrate, emarginate in two thirds of its length and, like on the intermediate tarsus, with onychium on its ventral side. Intermediate tarsus longer than mesotibia. Metatibia apart from the apical ridge with only one short lateral ridge, parallel to the apical margin of tibia. Each of the first and second segments of posterior tarsus with one ridge (Fig. 31). Outer terminal spur of metatibia reaching one third of the length of the inner one.

Male genitalia as figured (Figs 32, 33, 34).

Length from tips of mandibles to tips of elytra 2.4 - 2.5 mm, to tip of pygidium 3.3 - 3.4 mm.

NAME DERIVATION. This species is named after Dr. H. Roer from Naturhistorisches Museum "A. Koenig", Bonn.

DIFFERENTIAL DIAGNOSIS. The new species differs from all known species of the genus *Neomordellistena* Ermisch, 1950 in having only one lateral ridge on metatibia, the constant number being two in other species.

TYPE MATERIAL. Holotypus, male, SWA, Tsitsikamma Berge, Stormsriver, 3.12.1981, J. Klapperich leg. Allotypus, female, the same data; Paratypes 3 ex, the same data; all deposited in the Naturhistorisches Museum "A. Koenig", Bonn (one Paratype deposited in my collection).

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# The genus *Stenalia* from Oriental region (Coleoptera: Mordellidae)

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Received January 6, 1995, accepted February 9, 1995

Published June 22 1995

Taxonomy, new species, descriptions, key, Coleoptera, Mordellidae, Oriental region

**Abstract.** First records of the genus *Stenalia* Mulsant from Oriental region are given and following new species are described: *Stenalia namensis* sp. n., *S. pacholatko* sp. n., *S. dembickyana* sp. n. (all from Thailand), *S. tonkina* sp. n. (Vietnam) and *S. indica* sp. n. (India). Key to the Oriental species of *Stenalia* is given.

## INTRODUCTION

The genus *Stenalia* Mulsant, 1856 has been known only from Palaearctic and Afrotropical regions, the easternmost species having been *S. rufohumeralis* Pic, 1926 from Kamtschatka. The tribe Stenaliini has been represented in the Oriental region only by the genus *Brotskyella* Horák, 1989, which at present contains two species. One of them, *B. pectoralis* (Pic, 1923), was originally described as *Stenalia* by Pic (1923). In the present paper are given descriptions of five new species of the true genus *Stenalia* from Oriental region. As suggested by the configuration of ridges on posterior legs, all these species are related to the Afrotropical species of the genus (Franciscolo 1957) but, on the contrary, they have maxillary palpi of normal size (like Palaearctic species), not as minute as the Afrotropical ones. All new species were collected in rather dry areas of northern Oriental region and the discovery of further undescribed species in the zone between northern India and northern Vietnam can be expected.

## Acknowledgments

I wish to express my thanks to Dr C. Girard (Muséum d'Histoire Naturelle, Paris), who enabled me to study the material in his charge, as well as to my colleagues V. Kubák, P. Pacholatko, L. Dembicky (all Brno) and C. Holzschuh (Wien), who supplied me with the material, upon which new species were described.

## Key to Oriental species of *Stenalia*

- 1(6) Terminal spurs of metantra yellow to yellow-brown
- 2(2) Terminal segment of maxillary palpus in male short, quadrangular, its outer margin with additional rounded angle at two thirds of its length (Fig. 2). Antennae beginning from the fifth segment strongly serrate, each of the segments 6 - 9 almost three times as wide as the fourth one (Fig. 3). Length 5.8 mm. Thailand. *S. namensis* sp. n.
- 3(2) Terminal segment of maxillary palpus in male short, narrowly securiform, distinctly triangular (Figs 8, 16). Antennae filiform, each of segments 6 - 9 hardly twice broad as the fourth one (Figs 9, 17).
- 4(5) Eyes very broad, almost round, reaching posterior margin of the head. Temples not developed. Ventral margin of head of head strongly rounded below eyes (Fig. 11). Length 5.8 mm. Thailand. *S. pacholatko* sp. n.



- 5(4) Eyes oblong oval, narrowed anteriorly, not reaching posterior margin of head. Temples distinctly developed. Ventral margin of head almost flat below eyes (Fig. 19). Length 6.7 - 7.1 mm. Vietnam. *S. jankaea* sp. n.
- 6(1) Terminal spur of metatibia black.
- 7(8) Eyes not reaching posterior margin of head, temples narrow, but distinctly developed (Fig. 24). Maxillary palpi in both sexes narrow, second segment in male only slightly wider than the following ones (Fig. 21). Basal segment of anterior tarsi only slightly wider than the following ones (Fig. 23). Length 5.3 - 6.8 mm. Thailand *S. dembickiana* sp. n.
- 8(7) Eyes reaching posterior margin of head, temples completely missing (Fig. 32). Maxillary palpi strongly dilated, second segment in male by one third wider than the third one (Fig. 29). Basal segment of anterior tarsi in male swollen, distinctly wider than the following ones (Fig. 31). Length 5.2 - 6.2 mm. India (Bengal). *S. indica* sp. n.

*Stenalia siamensis* sp. n.

Slender and little convex (Fig. 1). Black, with yellowish elytra bordered with black both at sides and suture, palpi yellow, four basal segments of antennae, anterior legs and terminal spurs of metatibia yellowish brown. Pubescence black, becoming silvery on anterior portion of mesosternum and at the bases of abdominal sternites.

Head rather broadly convex, wider than long (as 6 : 5). Eyes broadly oval, not emarginate at insertions of antennae, very finely faceted, glabrous. Neither temples nor temporal angles developed. Second segment of maxillary palpus (Fig. 2) with a plate-shaped extension at the tip, by nearly one fifth wider than the third segment; terminal segment broadly securiform with strongly rounded anterior margin, so that it is nearly tetragonal with arcuate unequal sides (having a form of quadrangle with arcuate sides of unequal length). Antennae long (Fig. 3), beginning from the fifth segment strongly dilated and serrate; segment 1 by one third longer and slightly larger than 2, 3 very minute, by one third shorter and slightly narrower than 2, neighbouring segments, which are subequal; 5 by one third wider and somewhat longer than 4; segment 6 is the largest one, both longer and wider by one fifth than 5 and 1.3 times longer than wide; segments following the sixth one gradually diminishing, terminal segment oblong oval, almost twice as long as wide, by one third narrower and slightly longer than the penultimate one.

Pronotum moderately convex, rather parallel-sided, distinctly longer than wide (as 7.4 - 6.6). Anterior margin with slight collar-shaped protuberance. Sides (lateral view) emarginate, posterior angles rectangular. Dorsal surface densely and finely punctate.

Scutellum broadly triangular with silvery pubescence.

Elytra narrow, 2.7 times longer than their combined width, very little convex, parallel-sided at the base, from one third of their length gradually narrowed towards the separately rounded tips.

Pygidium elongate, triangular, flat, by one third longer than hypopygium.

Anterior tibiae gently curved inwards, without a calf-like swelling and longer hairs at the base. Basal segment of anterior tarsus slightly wider than tibia, as long as two following ones together; fourth segment rectangular, deeply bilobed, with onychium on ventral side. Mesotibiae strongly curved inwards, as long as middle tarsi. Metatibia (Fig. 4), besides an oblique apical ridge, with two oblique lateral ridges, first segment of hind tarsus with three ridges (upper one rudimentary), each of the second and third segments with one ridge. Outer terminal spur of metatibia almost as long as the inner one.

Male genitalia as figured (Figs 5, 6).

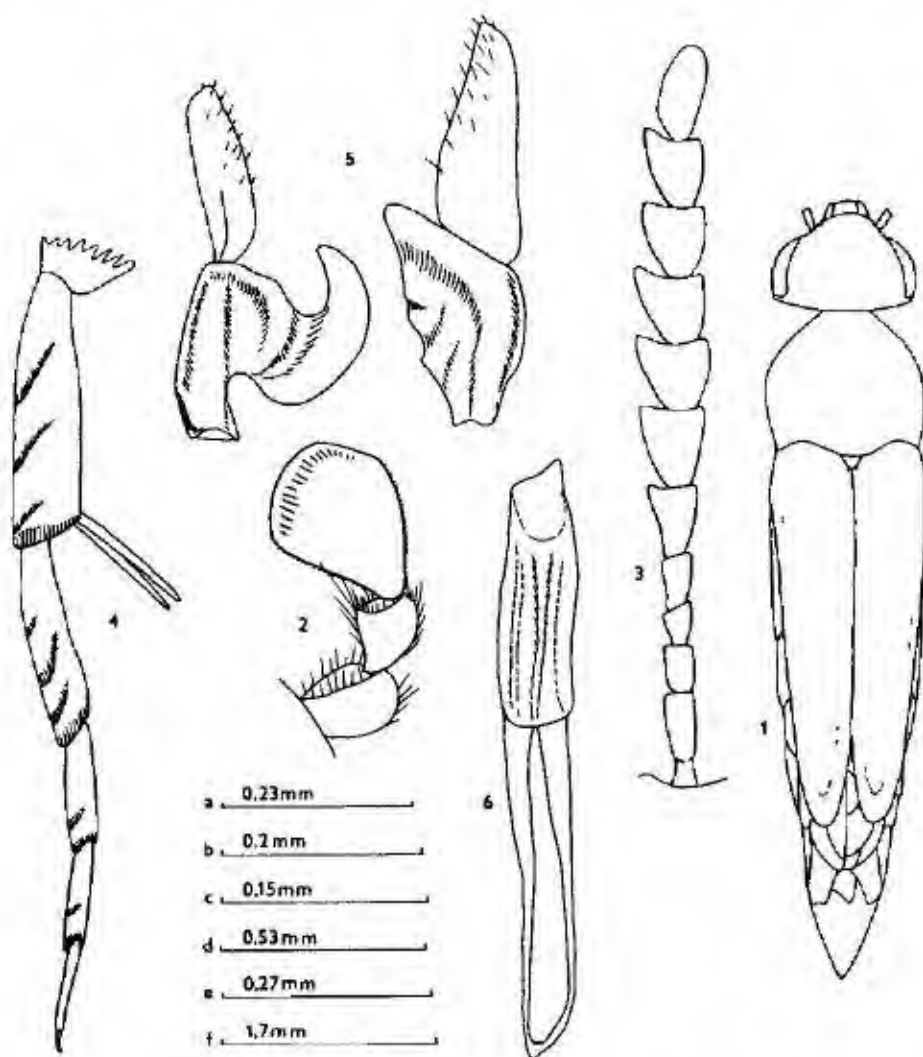
Length from tips of mandibles to tips of elytra 4.6 mm, to tip of pygidium 5.8 mm.

NAME DERIVATION. The specific name refers to country of origin - Siam (today Thailand).

TYPE MATERIAL. Holotype, male, Thai, Palong, 750 m. 19°55' N 99°06' E, 26-28.5 1991, Vlt. Kubán leg., deposited in my collection.



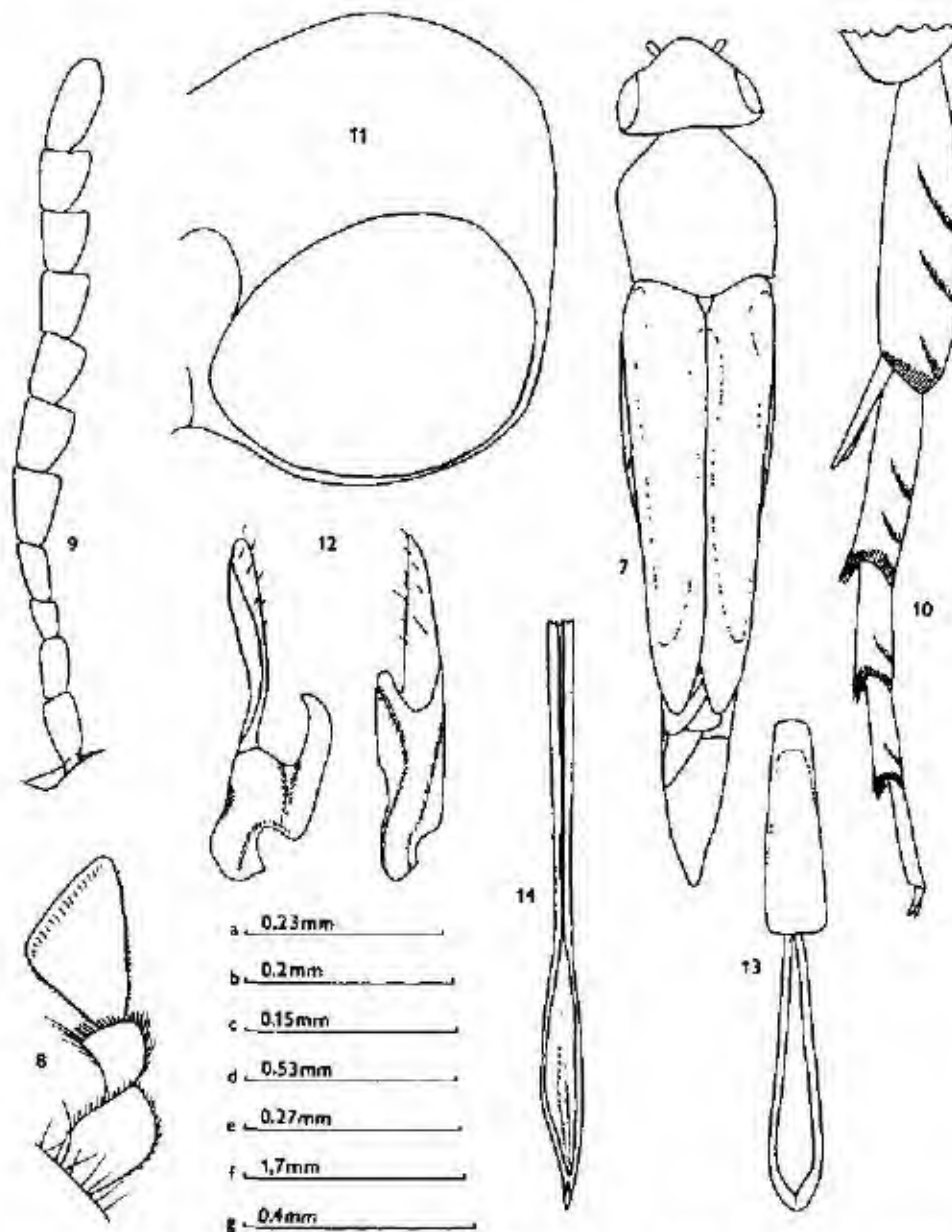
DIFFERENTIAL DIAGNOSIS For diagnostic characters see the above key to Oriental species of *Stenalia*



Figs 1-6 *Stenalia suamensis* sp. n. (holotypus, male) 1 - general view, 2 - maxillary palpus, 3 - antenna, 4 - posterior tibia and tarsus, 5 - left and right paramere, 6 - phallobase. Scale a - 4, b - 2, c - 5, d - 3, e - 6, f - 1

*Stenalia pacholatko* sp. n.

Slender and little convex species (Fig. 7). Black, yellowish elytra bordered with black at sides and along suture, palpi, four basal segments of antennae, maxillary lobes, fore legs and terminal spurs of metatibia brown-yellow, middle legs blackish brown. Pubescence black, on the anterior portion of mesosternum and bases of abdominal sternites silvery.



Figs 7-14 *Stenalia pacholarkoi* sp. n. (holotypus, male): 7 - general view, 8 - maxillary palpus, 9 - antenna, 10 - posterior tibia and tarsus, 11 - eye, 12 - left and right paramere, 13 - phallobase, 14 - penis. Scale: a - 10, b - 8, c - 12, d - 9, e - 13, 14, f - 7, g - 11

Head broadly convex, wider than long (as  $6:5$ ). Eyes broadly oval, not emarginate against insertions of antennae, very finely faceted and glabrous. Temples not developed (Fig. 11). Second segment of maxillary palpus in male strongly dilated (Fig. 8), plate-shaped, almost by one

third wider than the third, terminal segment broadly securiform, inner angle shifted from its midlength slightly towards the base; in female is the terminal segment narrowly securiform. Antennae (Fig. 9) of medium length, neither strongly dilated nor strongly serrate beginning from the fifth segment; segment 1 almost by one third longer and slightly wider than 2; 3 by one third shorter and distinctly narrower than 2; 4 by one third longer than and as wide as 3; 5 by one third longer and by one fourth wider than 4; 1.4 times as long as wide, segments beginning from the fifth one slightly gradually diminishing distally, so that the segment 10 only 1.2 times as long as wide; terminal segment oblong oval, 1.5 times as long as wide and by one third longer than the preceding one. Antennae in female narrower.

Pronotum rather flat, little convex, parallel-sided, longer than wide (as 7.2 : 6.5), anterior margin with distinct collar-shaped projection, more strongly developed in female. Sides (lateral view) deeply emarginate, posterior angles rectangular. Disc finely and densely punctate.

Scutellum small, broadly triangular, with silvery pubescence.

Elytra narrow, 2.7 times longer than their combined width, feebly convex, in basal fourth parallel-sided, separately rounded at apex.

Pygidium elongate, conical, flat, by one third longer than hypopygium, both pygidium and hypopygium shorter in female.

Protibiae in male strongly curved inwards, without calf-like swelling and without longer hairs at the base. Anterior tarsus, except for the last segment, as wide as tibia; first segment nearly as long as three following ones, fourth segment deeply bilobed with onychium on its ventral side. Mesotibiae strongly curved inwards and distinctly longer than tarsi. Metatibia (Fig. 10), besides a strongly oblique apical ridge, with two very oblique lateral ridges. First segment of posterior tarsus with two oblique ridges, each of the second and third segments with one ridge. Both terminal spurs of metatibia of equal length.

Male genitalia as figured (Figs 12 - 14).

Length from tips of mandibles to tips of elytra 4.6 mm, to tip of pygidium 5.5 - 5.9 mm.

NAME DERIVATION. The new species is named for one of its collectors and my friend Mr. Petr Pacholátko.

TYPE MATERIAL. Holotypus, male, Thai, Nanueng, 21.-26.5.1993, Pacholátko and Dembický leg.; Allotype, female, NW Thailand, Mae Hong Son distr., Ban Si Lang, 1200m, 23.-31.5.1991, J. Horák leg.; both deposited in my collection.

DIFFERENTIAL DIAGNOSIS. For diagnostic characters see the above key to Oriental species of *Stenalia*.

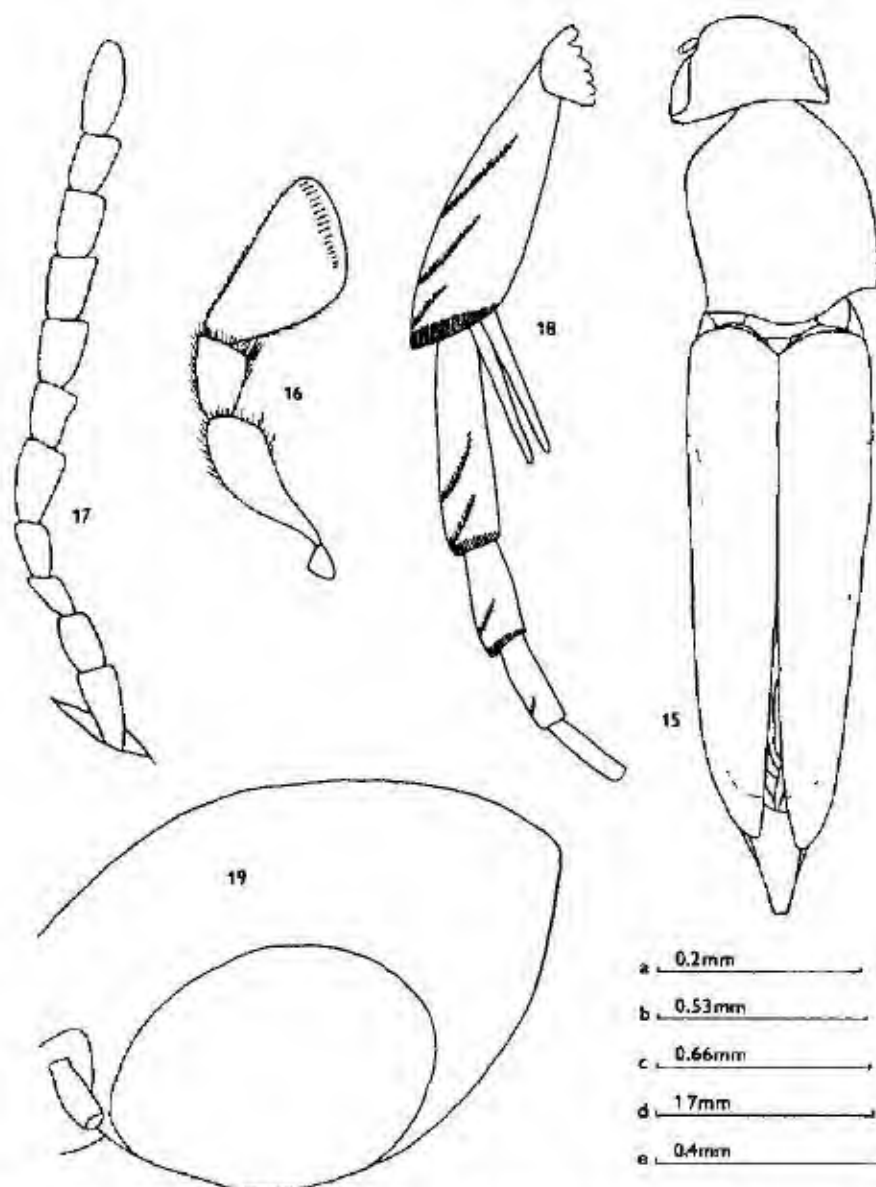
#### *Stenalia tonkinea* sp. n.

Slender and rather large species: 6.7 - 7.1 mm (Fig. 15). Black; maxillae, five basal antennal segments, terminal spurs of metatibiae and almost entire elytra yellow. Pubescence black apart from the silvery hairs on anterior portion of mesosternum and bases of abdominal sternites.

Head short, strongly convex, longer than wide (as 6.3 - 5.5). Eyes oblong oval, both above and below only moderately rounded, finely faceted and glabrous, not reaching posterior margin of head capsule. Temples distinctly developed (Fig. 19). Maxillary palpi (Fig. 16) in female yellowish brown, second segment somewhat wider than the third one; terminal segment elongate, securiform, inner angle situated between middle and two thirds of its length. Antennae (Fig. 17) rather long, narrowly serrate, with four to six basal segments yellow-brown.

Pronotum flatly convex, longer than wide (as 9 : 8). Anterior margin with distinct collar-shaped projection. Sides in lateral view strongly S-shaped, posterior angles rectangular.

Scutellum small, triangular, with silvery pubescence.



Figs 15-19 *Stenalia tonkinensis* sp. n. (holotypus, female) 15 - general view, 16 - maxillary palpus, 17 - antenna, 18 - posterior tibia and tarsus, 19 - eye Scale a - 16, b - 17, c - 18, d - 15, e - 19

Elytra, especially in the middle, strongly flattened, 2.8 times longer than their combined width, separately rounded at the apex, with very fine and dense rasp-like punctures. Surface of elytra yellow, black border very indistinct, basal portion completely yellow with yellow hairs, pubescence on the rest of elytra blackish.

Pygidium elongate, conical, flat, more strongly narrowed at the apex, almost twice as long as hypopygium.

Anterior tibiae distinctly shorter than and as wide as anterior tarsi, moderately curved inwards (female). First segment of anterior tarsus only slightly shorter than three following segments combined, penultimate segment subquadrate, deeply bilobed, with compact onychium ventrally. Middle tarsi shorter than mesotibiae. Metatibia (Fig. 18), besides oblique apical ridge, with two very oblique lateral ridges, the lower ridge being somewhat shorter than the upper one. First segment of posterior tarsus with two oblique ridges, each of the second and third segments with one ridge. Terminal spurs of metatibia yellow, subequal.

Length from tips of mandibles to tips of elytra 6.2 - 6.8 mm, to tip of pygidium 6.7 - 7.1 mm. NAME DERIVATION. The specific name refers to country of origin - Tonkin (today northern part of Vietnam).

TYPE MATERIAL. Holotype: female. Hon Binh, Tonkin, de Cooman leg., 278, bearing manuscript label 'Stenalia angustata'. Paratype: 1 female. Hoa Binh, Tonkin, both deposited in Muséum d'Histoire Naturelle, Paris.

DIFFERENTIAL DIAGNOSIS. For diagnostic characters see the above key to Oriental species of *Stenalia*.

*Stenalia dembickyana* sp. n.

Slender and little convex (Fig. 20). Black, maxillary palpi and four basal antennal segments blackish brown, elytra yellowish brown with very narrow indistinct black border and infusate tips. Pubescence black except for silvery hairs on anterior portion of mesosternum and on bases of abdominal sternites.

Head rather broadly convex, wider than long (as 7.3 - 6.3). Eyes broadly oval, not emarginate against insertions of antennae, very finely faceted and glabrous. Posterior margin of eye not reaching posterior margin of head capsule, temples narrow, but distinctly developed (Fig. 24). Second segment of maxillary palpus (Fig. 21) narrow, long, distinctly wider than the third one. Terminal segment in both sexes narrowly securiform, inner angle situated somewhat behind its midlength. Antennae (Fig. 22) medium-sized, dilated beginning from the fifth segment, which is twice as broad as the third one, segments 1 and 2 equally broad, 1 by one-fourth longer than 2, 3 slightly shorter and by one-third narrower than 2, as large as 4, 5 by one-fourth longer and by one-third broader than 4, segments beginning from the fifth one gradually abbreviated distally, fifth segment 1.4 times, tenth segment 1.2 times longer than broad, terminal segment oblong oval with narrowed distal end, as long as and only slightly narrower than the preceding one. Antennae equal in both sexes.

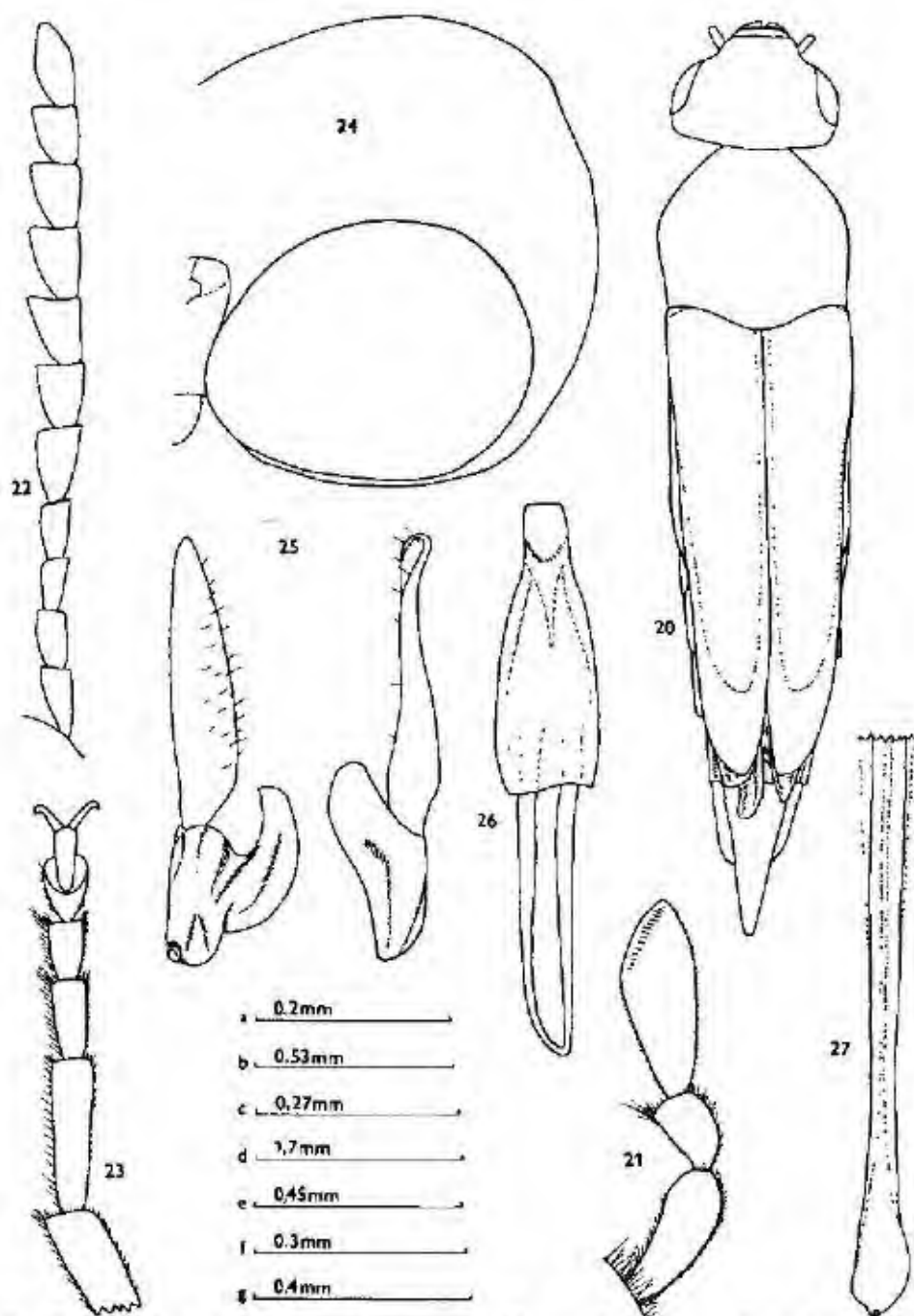
Pronotum moderately convex, rather parallel-sided, longer than wide (as 9 - 8). Anterior margin with slight collar-shaped projection. Sides in lateral view strongly emarginate, posterior angles rectangular. Disc finely and densely punctate.

Scutellum triangular, with silvery pubescence.

Elytra narrow, 2.5 times longer than their combined width, little convex, parallel-sided at the base, behind it gradually narrowed posteriorly, narrowly separately rounded at the apex.

Pygidium elongate, conical, flat, by one-third longer than hypopygium.

Anterior tibiae in male straight, without swelling and without longer hairs at the base, longer than anterior tarsi. First segment of anterior tarsus (Fig. 23) slightly narrower than tibia, as long as two following segments combined, fourth segment slightly longer than wide, wider than preceding segments, bilobed in two-thirds of its length and with rounded onychium ventrally. Mesotibiae strongly curved inwards, as long as middle tarsi. Metatibia, besides an oblique apical ridge, with two long and oblique lateral ridges, the upper ridge being distinctly longer than the lower one. Basal segment of posterior tarsus with three ridges (the uppermost ridge often rudimentary or even missing), each of the second and third segments with one ridge. Outer terminal spur of metatibia by one-fifth to one-sixth shorter than the inner one.



Figs 20-27. *Stenalia dembickyana* sp. n. (holotypus, male): 20 - general view; 21 - maxillary palpus; 22 - antenna; 23 - anterior tarsus; 24 - eye; 25 - left and right paramere; 26 - phallobase; 27 - penis. Scale: a - 21; b - 22, c - 26, 27; d - 20; e - 23, f - 25; g - 24.



Male genitalia as figured (Figs 25 - 27).

Length from tips of mandibles to tips of elytra 4.7 - 6.0 mm, to tip of pygidium 5.8 - 7.1 mm.

NAME DERIVATION. The new species is named for my friend Mr. Luboš Dembický, specialist to oriental Cerambycidae.

TYPE MATERIAL. Holotypus, male, NW Thailand, Mae Hong Son distr., Ban Huai Po, 1600 - 2000m, 17 - 23 V 1991, J. Horák leg.; Allotypus, female, the same data, Paratypes, 5 males (1 male deposited in Muséum d'Histoire Naturelle, Paris), the same data, all deposited in my collection.

DIFFERENTIAL DIAGNOSIS. For diagnostic characters see the above key to Oriental species of *Stenalia*.

*Stenalia indica* sp. n.

Slender, comparatively short and convex (Fig. 28). Black; maxillary palpi, four basal antennal segments, anterior femora and tibiae, posterior femora and elytra yellow-brown to brown. Elytra with indistinct black border and little infuscate tips. Black pigmentation may be suppressed on some body parts (e.g. legs, pronotum, abdomen), so that only head and terminal spurs of metatibia remain black. Pubescence of head, pronotum, scutellum, some parts of meso- and metasternum and at the base of the first abdominal sternite silvery, that of elytra golden-grey with pronounced golden sutural stripe; rest of body with grey-black hairs.

Head broadly convex, with than long (as 6 : 5). Eyes broadly oval, not emarginate against insertion of antennae, very finely faceted and glabrous. Temples not developed (Fig. 32). Second segment of maxillary palpus dilated (Fig. 29), wider than the third, terminal segment rather narrowly securiform, with inner angle shifted somewhat distally behind its midlength; palpi in female very narrow. Antennae (Fig. 30) of medium length, not dilated, particular segments subcylindrical; segment 1 by one fourth longer than and nearly as wide as 2; 3 narrower and shorter than 2, as wide as and slightly shorter than 4; 5 conical, by one third longer and by one fourth wider than 4; each of segments 5 - 10 1.3 times longer than wide; terminal segment oblong oval, moderately narrowed distally, 1.8 times longer than wide and by one fourth longer than the preceding one. Antennae in female somewhat shorter than in male.

Pronotum longer than wide (as 6.8 : 6), flatly convex, with very short collar-shaped projection, in basal third narrowed posteriorly. Sides in lateral view strongly S-shaped, posterior angles rectangular.

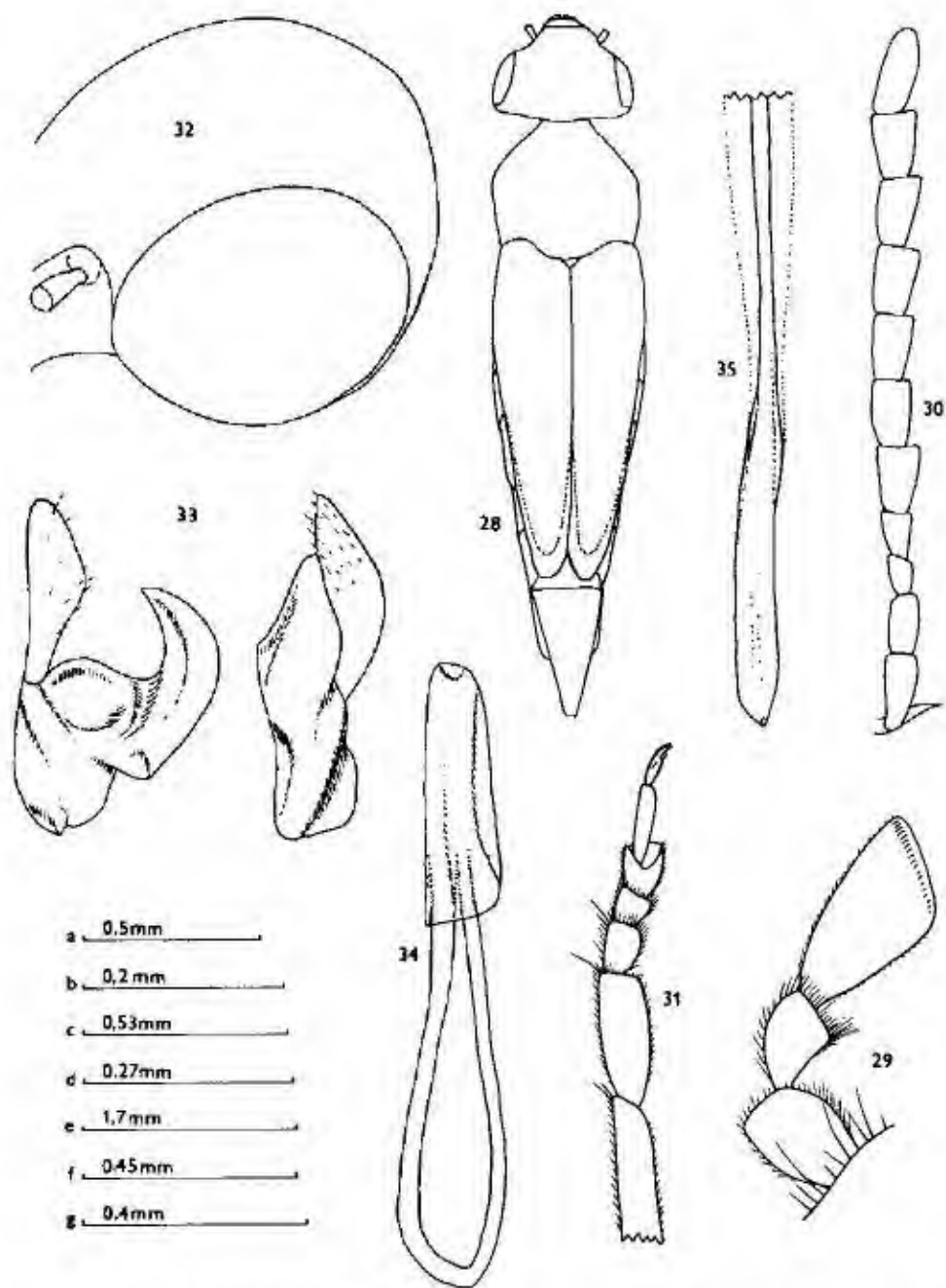
Scutellum minute, triangular, with silvery pubescence.

Elytra moderately convex, almost parallel-sided in basal third and then rather strongly narrowed posteriorly towards separately and narrowly rounded apex, 2.3 times longer than their combined width, with fine and dense rasp-like puncturation. Elytra reaching the midlength of penultimate abdominal segment in male, whereas covering it completely in female.

Pygidium in male rather narrowly conical, short and broadly conical in female, rather flat and by one third longer than hypopygium.

Protibiae straight, not dilated, at most with very indistinct longer hairs. First segment of anterior tarsi swollen (Fig. 31), as wide as tibia and wider than following segments, as long as three following segments combined; fourth segment somewhat longer than wide, emarginate in three fourths of its length, with simple onychium ventrally. Mesotibiae strongly curved inwards, shorter than middle tarsi. Metatibia, besides very oblique apical ridge, with two very oblique lateral ridges, which are of equal length and reach to the middle of tibia width. First segment of posterior tarsus with three ridges (upper one mostly rudimentary), each of the second and third segments with one ridge. Outer terminal spur of metatibia somewhat shorter than the inner one.

Male genitalia as figured (Figs 33 - 35).



Figs 28-35. *Stenalia indica* sp. n. (holotypus, male): 28 - general view; 29 - maxillary palpus; 30 - antenna; 31 - anterior tarsus; 32 - eye; 33 - left and right paramere; 34 - phallobase; 35 - penis. Scale: a - 33; b - 29; c - 30; d - 34, 35; e - 28; f - 31; g - 32.

Length from tips of mandibles to tips of elytra 4.2 - 5.7 mm, to tip of pygidium 5.2 - 6.6 mm  
NAME DERIVATION The specific name refers to country of origin - India

TYPE MATERIAL. Holotype, male, India, West Bengal, Distr. Darjeeling, Kalimpong, Dumry Busty 1000m, 8.4.1991,  
N. Dangal leg. Allotype, female, India, West Bengal, Distr. Darjeeling, Kalimpong, Khani Busty, 900m, 25.3.1991,  
N. Dangal leg. Paratypes: 1 male, the same data as Allotype, 1 female, India, West Bengal, Distr. Darjeeling, Kalimpong,  
Vah Dara, 600m, 26.3.1991. N. Dangal leg. all specimens deposited in my collection

DIFFERENTIAL DIAGNOSIS For diagnostic characters see the above key to Oriental species of *Stenaha*

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**A review of the Chinese *Aphodius* species (Coleoptera: Scarabaeidae).  
Part 1: subgenus *Agolius***

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Received January 16, 1995; accepted February 9, 1995  
Published June 22, 1995

**Taxonomy, new species, new status, new combination, distribution, Coleoptera, Scarabaeidae, *Aphodius*, *Agolius*,  
Palearctic region**

**Abstract.** Chinese and Himalayan species of *Aphodius* Illiger subgenus *Agolius* Mulsant & Rey are reviewed. *Aphodius* (*Agolius*) *takm* sp. n. is described from Sichuan and its diagnostic characters including male genitalia and epipharynx are illustrated. *A. (A.) orinus* W. Koshantschikov stat. n. is redescribed and raised to rank of valid species distinct from *A. (A.) haroldi* D. Koshantschikov. *A. (A.) haroldi* is for the first time recorded from China (Xinjiang). Chinese and Himalayan *Agolius* species are keyed.

INTRODUCTION

The species inaugurated taxonomical history of the subgenus *Agolius* is *Aphodius abdominalis* Bonelli described in 1812. Subgenus *Agolius*, established by Mulsant & Rey, 1869 for "fraction" of *Acrossus* Mulsant, 1842 with six species without designation of type, was subsequently revised by Reitter (1892) who designated *A. mixtus* A. & J. B. Villa, 1833 (= *A. abdominalis* Bonelli, 1812) as the type of this subgenus. The classification presented in this paper, it means classification of *Neagolius* W. Koshantschikov, 1912 as species group within subgenus *Agolius*, is that of e.g. Balthasar (1964) and Mariani (1979).

The subgenus contains presently 18 species (cf. Dellacasa 1988, Pittino & Ballerio 1994) inhabiting mostly alpine areas of Palearctic region. Most of them are at least facultatively saprophagous. Three species are presently known from China, the fourth species is described below.

Terminology concerning epipharyngeal structures was adopted from Dellacasa (1983).

The following abbreviation for material depositories are used in the text:

DKCP - Czech Republic, Praha, David Král collection

HNHM - Hungary, Budapest, Hungarian Natural History Museum (O. Merkl, G. Széll)

MHNG - Switzerland, Genève, Muséum d'Histoire Naturelle (J. Lohr)

MNHN - France, Paris, Muséum National d'Histoire Naturelle (Y. Camberfort, Th. Deuve)

NHMB - Switzerland, Basel, Naturhistorisches Museum (M. Brancucci)

NMPC - Czech Republic, Praha, National Museum (Natural History) (J. Jelínek)

RCCP - Czech Republic, Praha, Radek Červenka collection

I am very grateful to all above mentioned colleagues for enabling me to study material deposited in their institutions or private collections. I am also much obliged to following friends, who provided me with interesting material: L. Boček (Olomouc), K. Křehák & B. Březina (Praha), M. Kafka (Neratovice, CZ), J. Kolář (Brno), J. Kaláb (Brno) and J. Turna (Kostelec na Hané, CZ).

# Key to *Agolius* species known from China and Himalaya

- 1 (2) Pronotal basis completely bordered. Terminal spur of protibiae in male shortened, stout and bent down- and inwards. Elytra yellowish brown, mostly with dark spots. Xinjiang, Gansu.  
*A. (A.) fulcispinus* W. Koshantschikov
- 2 (1) Basal border of pronotum at middle broadly interrupted. Terminal spur of protibiae in male simply acute. Elytra entirely reddish brown to black without dark spots.  
*A. (A.) lorinus* W. Koshantschikov stat. n.
- 3 (4) Elytra shagreened, nearly alutaceous. Basimetatarsite distinctly longer than upper terminal spur. Female unknown. Himalaya (Himachal Pradesh).  
*A. (A.) montisjaldi* Puttino comb. n.
- 4 (3) Elytra shiny, not shagreened. Basimetatarsite equal in length or shorter than upper terminal spur.
- 5 (6) Basimetatarsite distinctly shorter than upper terminal spur. Body reddish brown with frontal and elytral sutures. Elytral disc and two small irregular spots at each pronotal side darker brown. Female unknown. Xinjiang (Jildus mts.).  
*A. (A.) hamidi* D. Koshantschikov
- 6 (5) Basimetatarsite equal in length to upper terminal spur. Body entirely brown to black.
- 7 (8) Anterior clypeal margin approximately subtruncate, not distinctly sinuate at middle. Pronotum simply, sparsely punctate, punctures separated by more than twice their diameter. Elytra finely setaceous apically and laterally. Elytral intervals flat. striae punctures not crenating intervals margins. Sternites with long setae. Xinjiang (Borchhor mts.).  
*A. (A.) tukan* sp. n.
- 8 (7) Anterior clypeal margin distinctly sinuate at middle. Punctuation of pronotum double, consisting of coarse punctures separated by about twice their diameter, mixed with rather fine ones, separated by more or less their diameter. Elytra entirely glabrous. Elytral intervals moderately convex, striae punctures remarkably crenating intervals margins. Sternites with short setae. Female unknown. Sichuan (Minshan mts.).  
*A. (A.) tukan* sp. n.

## *Aphodius (Agolius) fulcispinus* W. Koshantschikov, 1912

*Aphodius (Neagolius) fulcispinus* W. Koshantschikov, 1912: 517, fig. 3, A. Schmidt, 1922: 218, Boucomont, 1929: 779, G. Dellacasa, 1983: 324-325, figs 728-732, M. Dellacasa, 1988: 386.

*Aphodius (Melinopterus) pallidicinctus*: Reitter, 1882: 237, nec Waterhouse, 1875: 85.

*Aphodius (Agolius) fulcispinus*: Balthasar, 1964: 150, Manani, 1979: 84, Nikolajev & Punsagdulam, 1984: 145, fig. 31.

RESTRICTED TYPE LOCALITY: "In den Bergen des Chinesischen Turkestan" (Dellacasa 1983).

MATERIAL EXAMINED: China, Xinjiang autonomous region: Ost-Turkestan, Altyn-Tagh, 7 1903, coll. Hauser, 3 males in MHNG; Gansu province: China, Kansu, coll. R. Petrovitz, 1 male in MHNG; Mongolia: Chasatyn-java Pass, Ajmak Bajan-Ulgii, 48° 30' N / 90° 42' E, 2580 m, 24.7.1964, Mongolisch-Deutsche Biolog. Exped. 1964, 1 female in HHNM; Mongolia, Central Aimak, SO von Somon Bajan-zogot, 1600 m, Nr. 520th, 11.6.1966, 2 males in HHNM; Mong. b., Ulsanbaatar: Tuf valley, 27.6.90, horse dung, David Král leg., 1 male in DKCP; Kazakhstan: Zaysan [lake], coll. Leonhard, 1 male in MHNG; Russia: Tuva [autonomous region], Mugur Aksu, 21.7.71, B. Korotajev [label written in Cyrillic script], 1 male and 2 females in RCCP.

DIAGNOSTIC CHARACTERS: Rather plump, light coloured species, elytra yellowish brown, mostly in male with dark spots, in female without these spots. Head small in size, anterior clypeal margin subtruncate, anterior angles rounded. Pronotal basis completely bordered, punctuation of pronotum double. Elytral humeri without teeth, intervals only very slightly convex, striae punctures remarkably crenating intervals margins. Elytra microscopically setaceous apically. Sternites shortly setaceous. Terminal spur of protibiae in male shortened, stout and bent down- and inwards, in female simple acute, under terminal spur of mesotibiae in male not shortened, basimetatarsite distinctly shorter than upper terminal spur. For aedeagus and epipharynx see figures 730-732 in Dellacasa (1983).

DISTRIBUTION: China: Xinjiang, Gansu, Qinghai, Mongolia, Kazakhstan and southern parts of Siberia.

*Aphodius (Agolius) haroldi* D. Koshantschikov, 1894

*Aphodius (Agolius) haroldi* D. Koshantschikov, 1894, 98; A. Schmidt, 1922: 107-108, 111; Balthasar, 1964: 146-147, Mariani, 1979: 83, figs 46, 47, Stebnicka, 1989: 19, figs 25-27

*Aphodius (Neagolius) haroldi* Nikolajev, 1987: 113, M. Dellacasa, 1988: 386; Pittino, 1988: 115.

TYPE LOCALITY. Ketmen - Gebirge (Koshantschikov 1894).

MATERIAL EXAMINED. China, Xinjiang autonomous region: China, Xinjiang, W. Borohoro Shan [mts], Sayram lake, 28 VII 1993, 1 male in DKCP. Kazakhstan: Turkestan, Aulie Ata [=Dzhambul], coll. Reitter, 1 male in HHNM, SO Kazakhstan, Ketmenj G. - K. [mts], Ung. V. Ketmenj, 2000-2500 m, W. Dolm lgt., 1 male in DKCP, 2 males in NHMB, USSR - Kazachst., Alma Ata, Medeo, 22-29.6.1985. Dr J. Doskočil [lgt.], 1 male in DKCP; SSSR, Zaalyský Ala Tau [mts], Čimbulak, 3000-3400 m, 1 VII 1985, lgt. Mašek, 4 males in DKCP, SU - Kazakhstan, Panfilov [=Dzharkent], Dzhungarsky Alatau, 44° 30' [N], 79° 30' [E], 20-28.6.1991, 2500 m, M. Kafka lgt., 1 male in DKCP. Kirgizia: Turk. Sussamyr Geb. [mts], Ketmen-Tjube, 6.06., coll. Hauser, 2 males in MHNG, 1 male in HHNM; SU - Kirgizia, Grigoryevka, Kungey Alatau [mts.], 3000 m, 42° 50' [N], 77° 15' [E], 6-10.7.1991, M. Kafka lgt., 1 male in DKCP. Turkestan, Reitter, 1 female in HHNM.

DIAGNOSTIC CHARACTERS. Subparallel, rather plump, dark coloured species. Dorsal surface shiny and glabrous except of microscopically setaceous apical and lateral part of elytra. Head small in size, wide semicircular, anterior clypeal margin almost not sinuate. Pronotal basis not completely bordered, punctation of pronotum simple. Elytral humeri without teeth. Elytral intervals flat, striae punctures not crenating intervals margins. Metasternal plate shiny and glabrous with completely developed medial furrow, sparsely and almost regularly punctated throughout. Sternites with long setae. Terminal spur of protibiae in both sexes simply acute. Lower terminal spur of mesotibiae in male shortened (about half as long as upper one) and simply acute. Basimetatarsite equal in length to upper terminal spur. For aedeagus and epipharynx see figures 25-27 in Stebnicka (1989).

DISTRIBUTION. First record from China (Xinjiang); Kazakhstan, Kirgizia.

*Aphodius (Agolius) montisjuldii* Pittino, 1988 comb. n.

*Aphodius (Neagolius) montisjuldii* Pittino, 1988: 113-115, figs 2, 7, 8, M. Dellacasa, 1988: 386

TYPE LOCALITY. Thien-Shan, Juldus Geb. (Pittino 1988)

DIAGNOSTIC CHARACTERS. A member of *A. (Agolius) haroldi* group. Subparallel, rather plump, shiny, reddish brown, with frontal and elytral sutures, elytral disc and two small irregular spots at each pronotal side darker brown. Dorsal surface glabrous, except of posterior half of elytral sides as well as apical declivity with very short, scarce, inconspicuous setae. Head small in size, anterior clypeal margin subtruncate, slightly sinuate at middle. Basal border of pronotum at middle interrupted, punctation of pronotum simple, irregular, rather sparse, separated by about twice their diameter on disc; coarser and closer, separated by less than once diameter, laterally. Elytral intervals almost flat on disc, moderately convex basally as well as apically. Strial punctures slightly crenating intervals margins. Metasternal plate smooth, shiny, glabrous, with complete midline furrow and rather sparse punctures throughout. Sternites shagreened, with short, recumbent setae. Terminal spur of protibiae stout, lanceolate, roundly pointed. Lower terminal spur of mesotibiae blunt apically and shortened (about one third as long as upper one). Basimetatarsite slightly shorter than upper terminal spur. Parameres with outstanding membranous apical appendices - figs 7, 8 in Pittino (1988). Epipharyngeal structures not studied. Female not known.



**DISCUSSION.** This species has been described from a single male collected in eastern (Chinese) part of the Tian Shan mts. Holotype is preserved in coll. Pittino and was not studied by the author. Diagnostic characters above were selected from original description (Pittino 1988). This species belongs in *A. (A.) haroldi* species complex and can be easily distinguished by the external characters used in the above key. In addition, it is so far known only existing species of this species group with such outstanding apical membranous appendices of parameres.

*Aphodius (Agolius) orinus* W. Koshantschikov, 1912 stat. n. (Figs 5, 6)

*Aphodius (Agolius) haroldi* var. *orinus* W. Koshantschikov, 1912: 516-517; A. Schmidt, 1922: 112; Balthasar, 1964: 146; Mariani, 1979: 43; Stebnicka, 1989: 19.

*Aphodius (Neagolius) haroldi* subsp. *orinus*: M. Dellacasa, 1988: 386.

**TYPE LOCALITY.** Himalaya Gebiet, Rotang Pass (Koshantschikov 1912).

**MATERIAL EXAMINED.** India (Himachal Pradesh prov.): Vallée du Rotang (Himalaya), Juin 1914, G. Babault [igt.], 1 male in MNHN.

**DIAGNOSIS.** A member of *A. (Agolius) haroldi* group. Rather plump, brownish coloured species. Dorsal surface of head and pronotum moderately shiny, glabrous. Elytra shagreened, nearly alutaceous, microscopically setaceous. Head small in size, wide semicircular, anterior clypeal margin almost not sinuate. Pronotal basis not completely bordered, punctation of pronotum double, on disc sparse, becoming dense laterally. Elytral humeri without teeth. Elytral intervals flat, finely punctate, stria punctures not crenating intervals margins. Metasternal plate shiny, setaceous laterally, with completely developed medial furrow, sparsely punctate throughout. Sternites with long setae. Terminal spur of protibiae pointed, lower terminal spur of mesotibiae shortened and simply pointed. Basimetatarsite longer than upper terminal spur.

**REDESCRIPTION.** Male. Length 6.3 mm. Subparallel, rather plump. Head and pronotum shiny. Elytra nearly alutaceous, with microscopic setae. Colour entirely brownish.

Head wide, semicircular, almost without anterior clypeal sinuation; clypeal margin distinctly upturned, sides regularly broadly rounded, slightly notched before genae. Genae rounded, exceeding distinctly eyes outwards, with tuft of fine, long setae. Epistomal hump not developed, frontal suture distinct, with barely perceptible tubercles. Punctures of clypeal surface simple, coarse, dense, separated by less than their diameter. Punctation of frontal area a little finer.

Pronotum moderately convex, scarcely narrowed anteriorly, anterior angles widely rounded and only slightly projecting anteriorly, sides weakly diverging over anterior third, then almost straight, subparallel; posterior angles broadly rounded. Anterior margin and basis without border, lateral margin distinctly bordered, marginal furrow prolonged basally along posterior angle reaching level of elytral stria 6. Punctation of disc simple, irregular, coarse and sparse, punctures separated by about twice their diameter, becoming more dense basally. Lateral parts of pronotum with double punctation consisting of coarse, regularly distributed punctures separated by approximately their diameter and mixed irregularly with distinctly finer ones.

Scutellum triangular, longer than wide, impunctate.

Elytra scarcely dilatate posteriorly, widest just behind middle, without humeral teeth; striae distinctly impressed, stria punctures fine, separated by more than their diameter and becoming closer apically, not crenating intervals margins. Intervals almost flat, shagreened, almost alutaceous, with fine, sparse and irregularly distributed punctures; intervals 1 and 2 strongly narrowed apically, interval 3 uniformly wide over its length.

Metasternal plate smooth, shiny, setaceous laterally, with completely developed medial fur-

row; sparsely, nearly regularly punctate throughout. Abdominal sternites shagreened, slightly alutaceous, with long, hairlike setae.

All femora shiny, with sparse and fine punctures and long, hairlike setae. Terminal spur of protibiae stout, pointed apically, bent ventrally and reaching middle of protarsid 2. Lower terminal spur of mesotibiae shortened (about half as long as upper one) and simply pointed. Basimetatarsite longer than upper terminal spur.

Aedeagus as figured (Figs 5, 6).

Epipharyngeal characters not studied.

Female not known.

**DISCUSSION.** This species has been described by W. Koshantschikov (1912) as a variety of *A. (A.) haroldi*. Types (at least 2 specimens - in Koshantschikov (1912) with two different localities - "Rotang Pass" and "Cashmir") are probably preserved in Sankt Petersburg museum and were not studied by the author. The above redescription is based on one male (MNHN) that is taken from the same locality as at least one of types. External characters including different shape of aedeagus confirm this taxon to be a valid species. This opinion is indicated also in Stebnicka (1989).

*Aphodius (Agolius) takin* sp. n. (Figs 1 - 4)

**TYPE MATERIAL.** Holotype - male, labelled China, Sichuan, 19 VI 1992, 50 km NEE Songpan, ca 3500 m, in DKCP. Paratypes: Nos 1-3 - males: the same data as in the holotype (DKCP). No 4 - male, labelled China / NW Sichuan, 103. 50 [N] / 33. 10 [E], Mu Shan Mts., 2500-4500 m, 14 - 16. 07. 1990, in DKCP; No 5 - male, labelled China, N Sichuan, Jiozhagou, 3100 m, 13 - 15 Jun 1992, in DKCP; No 6 - male, labelled Sichuan, Huanglong, VI. 87, T. Deuve, M. Perac 1gr, in MNHN. Nos 7-12 - males, labelled China, Sichuan (Luxian), Zhagushan pass, environs 31. 50N/102. 40E, 4100-4600 m, alp. meadow, rhododendrons, 27 VI 1994, in DKCP; Nos 13-14 - males, labelled China, W Sichuan, 3500 m, road Sabde-Julong, pass 40 km N Julong, 22-23. 6. 1994, alpine region, in DKCP.

**DIAGNOSIS.** Member of *A. (A.) haroldi* group. Dark coloured species, dorsal surface entirely shiny and glabrous. Head small in size, anterior clypeal margin distinctly sinuate, anterior clypeal angles rounded. Pronotal basis not completely bordered, punctuation of pronotum double. Elytral humeri without teeth, intervals moderately convex, striae punctures remarkably crenating intervals margins. Sternites shortly setaceous. Terminal spur of protibiae acute, lower terminal spur of mesotibiae not shortened, basimetatarsite equal in length to upper terminal spur.

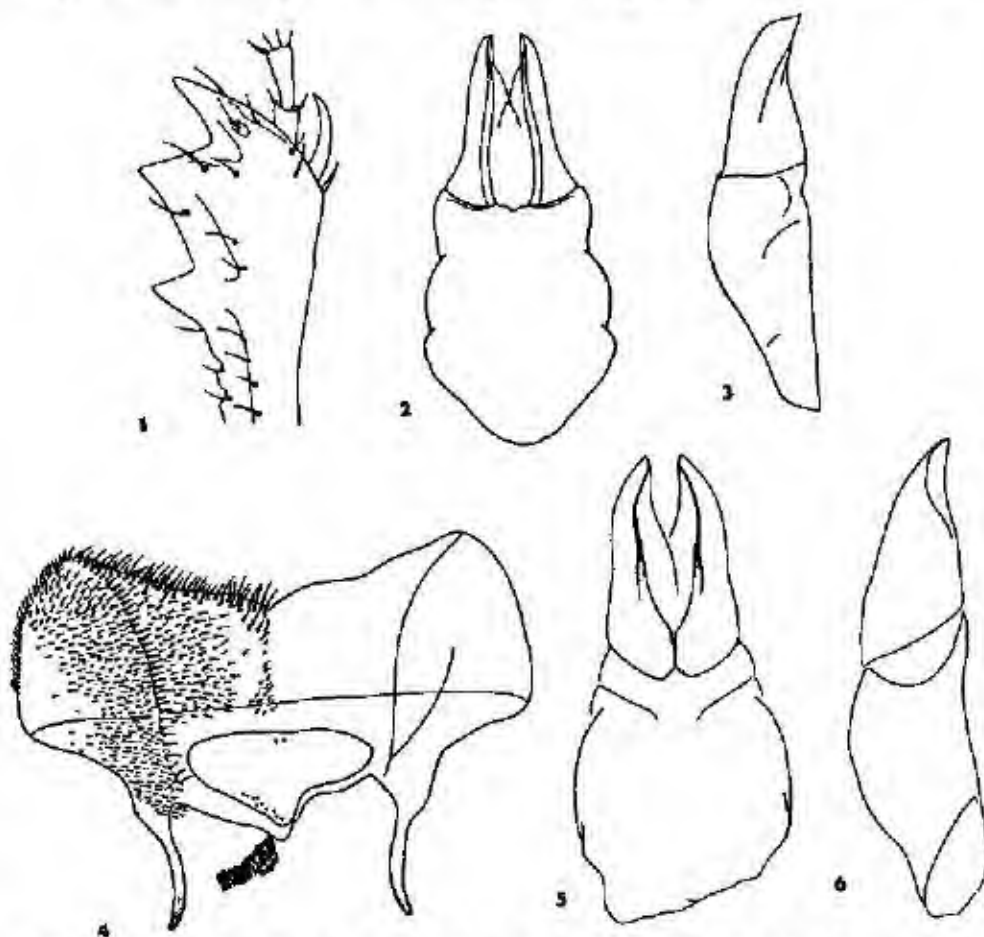
**DESCRIPTION.** Male. Length 5.8 - 6.4 mm. Subparallel, rather plump, moderately shiny. Colour blackish-brown, anterior angles of pronotum, humeral, sutural and apical part of elytra and appendages dark brown to reddish-brown. Dorsal surface entirely nude.

Head almost semicircular; anterior clypeal margin distinctly sinuate at middle, anterior angles widely rounded, almost indistinctly upturned, sides regularly broadly rounded, slightly notched before genae; genae rounded, distinctly exceeding eyes outwards, with tuft of fine setae. Clypeal surface moderately depressed near anterior angles; medial frontal hump slightly developed; frontooccipital suture invisible; punctures simple, coarse, separated more or less by their diameter.

Pronotum moderately convex, wide subparallel, scarcely narrowed anteriorly; anterior angles rounded, slightly projecting anteriorly; sides weakly diverging over anterior third, then almost straight, subparallel; posterior angles broadly rounded. Anterior margin and basis without border, lateral margins distinctly bordered, marginal furrow prolonging basally along posterior angle, reaching elytral stria 6. Punctuation of all surface double, consisting of coarse, rather irregularly distributed punctures, separated by about twice their diameter, mixed with finer ones, separated by their diameter.

Scutellum triangular, longer than wide, impunctate.

Elytra moderately dilatate posteriorly, widest just behind middle, without humeral teeth; striae distinctly impressed, stria punctures slightly but not remarkably crenating intervals margins, separated by about once their diameter, becoming closer near apex. Intervals moderately convex, with very fine and sparse punctures arranged in two longitudinal rows; intervals 1 and 2 uniformly wide over their length, others distinctly narrowed apically.



Figs 1-6. Left protibia (1), aedeagus - dorsal view (2, 5), aedeagus - lateral view (3, 6) and epipharynx (4) of: *Aphodius (Agolus) takin* sp. n. (1-4) and *A. (A.) orinus* stat. n. (5, 6).

Metasternal plate smooth, shiny and glabrous, with completely developed medial furrow and sparse irregular punctures throughout. Abdominal sternites shagreened, almost opaque, with short, recumbent hairlike setae.

All femora shiny very sparsely and finely punctate, and with long hairlike setae along femoral sides. Protibiae with three wide, distinctly protruding outer teeth; apical spur simple, stout, acute apically, bent down- and outwards, reaching hardly middle of protarsid 2 (Fig. 1). Meso- and metatibiae with well developed outer transversal carinae and setae unequal in length.

Basimesotarsite equal in length to upper terminal spur, lower terminal spur simply pointed  
 Basimetatarsite equal in length to upper terminal spur and subequal to next three metatarsites combined

Aedaeagus See Figs 2, 3

Epipharynx (Fig. 4) Epitorma slightly sclerotized. Setae of chaetoparia equal in length, long and thick. Acroparia and chaetopodium with moderately long and thin setae. Helus with short setae.

Female unknown

AFFINITIES The new species is related to *Aphodius (Agolius) haroldi*. For the differentiation see the complex of diagnostic characters in the key above.

CIRCUMSTANCES The new species was collected on alpine pastures (2500 - 4600 m a.s.l.) in dung of domestic herbivorous animals (*Bos*, *Equus*, *Ovis*), paratypes Nos 7-12 were collected under stones.

NAME DERIVATION Takin (*Budorcas taxicolor* Hodgson) is large herbivorous bovine animal inhabiting also area of this new *Aphodius*, noun in apposition.

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## Archaeozoological records of elk (*Alces alces*) in the Czech Republic

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Received December 22, 1994; accepted February 9, 1995  
Published June 22, 1995

Archaeozoology, palaeozoogeography, Holocene, hunting, Mammalia, *Alces alces*, Czech Republic

**Abstract.** Fragments of elk bones, teeth and antler were determined in thirteen (13) archaeozoological samples from archaeological excavations within the Czech Republic. Elk remains are supposed to be the result of local hunting by agricultural inhabitants. Findings reveal spatial and diachronic clusters. Elk bones were found in three neolithic sites situated in the western half of Bohemia. Nine sites, dating between the 5th and 14th century, are scattered over agricultural lowlands. The largest sample is reported from a site situated in NE Moravia (c. 2nd/1st cent. BC). This fortified settlement received special status and was situated in an elevated area outside the settlement oikumene, being geographically open to Poland. There is a gap in the evidence between c. 4000 BC and 150 BC, despite the fact that intensive hunting activities took place in the beginning of the 4th millennium. The latest evidence comes from the 14th century.

### INTRODUCTION

Analyses of bones from archaeological excavations carried out over the past few decades provided numerous results. The occurrence of species, animal use and forms of domestic and wild animals in different time periods allow us to reconstruct their spatial distribution and diachronic development. These analyses thus provide valuable data for palaeozoogeographical reconstructions. Archaeozoological samples, eg. different animal parts (teeth, bones, antlers, shells, etc.) obtained from archaeological excavations, were deposited as a result of human activity in different past time periods. They are always connected with particular archaeological cultures and thus are relatively precisely dated. Since the Neolithic period (after 5500 BC) the majority of remains are represented by the bones of domestic animals. Wild animals form only a minor part, indicating the additional value of hunted animals in human subsistence. The occurrence of wild animals in archaeological samples is influenced by a number of factors, including the following: - prehistoric bones mainly survive in calcareous areas (the acidic soils in the southern half of Bohemia lead to their rapid weathering), - not all species were edible, attractive for hunting or easy to encounter. Human settlements were situated mostly in the lowlands, not exceeding 300 m above sea level. With a few exceptions, most prehistoric cultures were not oriented towards hunting. Occasional hunting probably took place close to the settlements, but the size of their appropriate catchment area may have varied between different settlements/cultures, and remains unknown. Hunting practices were always influenced by ritual schemes, probably differing between different cultures. We can expect that many taboos existed concerning the consumption of wild animals. Different butchery practices and taphonomic transformations may have also altered the numerical proportions of the identified species. Thus the distribution maps for particular wild species are always more or less biased.



## MATERIALS AND METHOD

The author has collected all evidence for the presence of elk within archaeological samples in Bohemia and Moravia. A critical revision of bone fragments from published samples has been made, wherever possible. Table 1 presents a list of all 13 sites with bone samples containing elk remains. Sites are listed in diachronic order with their archaeological cultures, the total number of identified bones, the percentage of red deer remains (as a relative indicator of hunting activity), the number of elk remains and the minimum number of individuals which they represent. In the last two columns anatomical determinations as well as the information source (including unpublished data) are presented. In the case of the site of Stará Kouřim, its osteological material was destroyed and a re-analysis of the data is thus impossible.

## RESULTS AND DISCUSSION

Little archaeozoological evidence is available for the Mesolithic period (8000-5500 BC) in the Czech Republic. From the Neolithic period, wild animals generally form less than 10% (mostly only 1 to 5%) of total counts in bone samples from Central Europe. There is principally only one longer period (Late Neolithic/Early Eneolithic, c. 4000-3500 BC) where really large percentage of hunted animals occur. Similar proportions are also reported as an exception from a few sites in other prehistoric cultures.

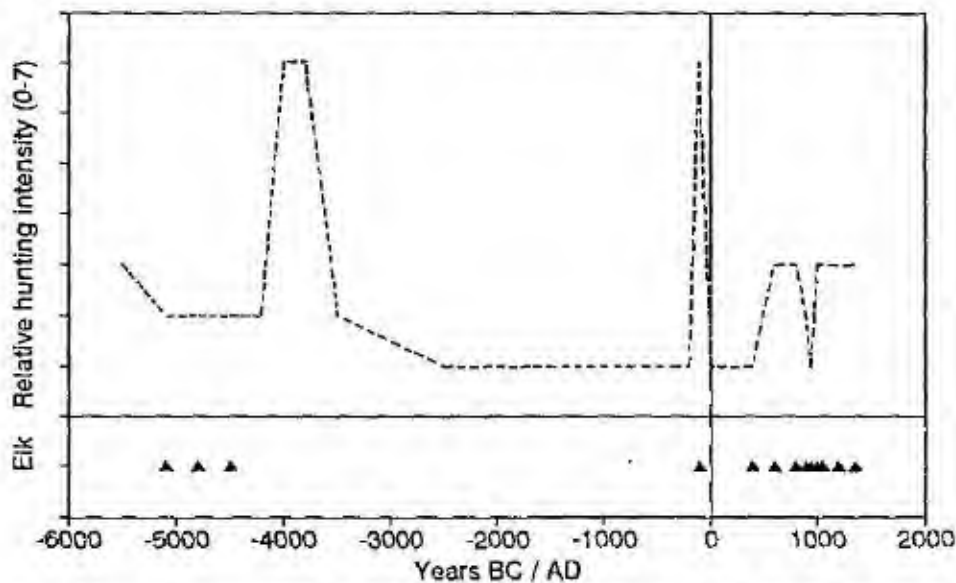


FIG. 1. Upper graph shows estimated relative intensity of hunting activity (in 8 classes based on red deer evidence) since the Neolithic. The lower part shows the approximate time distribution of elk remains.

Traditional hunted mammals, similar to those known from the Middle Ages, such as red deer, roe deer, boar, hare and Galliform birds, dominate the overall percentage of wild animals on all sites in Central Europe. Aurochs (*Bos primigenius*), bear (*Ursus arctos*), beaver (*Castor fiber*) and other fur animals were less frequent. The most rarely hunted mammals in the samples were wolf (*Canis lupus*), lynx (*Lynx lynx*), European bison (*Bison bonasus*), wild equids (*Equus* sp., *Asinus hydruntinus*) and elk (*Alces alces*).

Sites with evidence of elk form two separate groups according to both temporal as well as spatial dimensions. Through time (Fig. 1, lower part) there is clear evidence for elk hunting in the



Table 1. Sites with evidence of elk (*Alces alces*). In columns: archaeological culture, name of site (used in archaeological literature), number of context with A a, total sum of determined bones, percentage of red deer finds, number of A a finds, minimum number of A a individuals, anatomical part, source (m - various sites, n - research report in archive of Arch Inst Prague p - Peške in prep, 1 - Peške 1987, 2 - Čížmář et al 1981, 3 - Kratochvíl 1969, 4 - Novotný 1966, 5 - Peške 1986, 6 - Bučková 1956) and number in Fig. 2

Culture (period)	Site (parish)	Context No (phase)	Bone sum n	Deer %	Elk	Anatomical parts	Sc	No
Neolithic LaK	Chotěbuzice		957	3.8	1/1	Humerus dist	1	63
Neolithic SiK	Kopisty	392/70-1	?	?	2/1	Mic prox sin Mtt dist (-2yr)	n	62
Neolithic	Křimice	44/74	?	?	2/1	Radius prox dex Radius dist dex	n	25
Eneolithic	various sites		+5000	18.0	0		p	
Bronze	various sites		+15000	0.7	0		m	
Hallstatt	various sites		+10000	0.4	0		m	
la Tene	Požaha (Kojetín)		3405	17.0	9/3	Molar, 2xHumerus dist Radius, 2xTibia dist Mtp fr., PhI, PhII	p	39
Migration	Holubice		burial		1/0	Cornu	2	13
Early Slav	Běchovice	28/68	?	?	1/1	M3 inf sin	n	P
Slav	Pohansko		19250	0.6	1/1	PhI	3	37
Slav	Stará Kouhm	(9-10th c)	?	+	+		4	22
Early Medieval	Vyšehrad	344/31	892	0.8	2/1	PhI, PhIII	n	P
Early Medieval	Kouhm	147/69 345/70 409/70 610/70	3659	3.8	7/1	Mtpt Molar, PhII Mdb with M3, Mdb fr Cornu fr Ulna	5	22
Early Medieval	Hradsko	438/72	2883	3.6	1/1	Mtpt (artefact)	5	15
Early Medieval	Budeč	377/77	21205	0.3	1/1	PhII	5	8
Medieval	Lubice	(14th c)	?	?	1/1	?	6	26

Neolithic, but not at all in the beginning of the Eneolithic, a period well known for its intensive hunting activity (see for comparison the figures for the Eneolithic, as well as Bronze and Hallstatt periods in table 1 and the upper curve in Fig 1). The second and main group covers mainly the period of about one thousand years between 400-1300 AD.

Numerous finds from the la Tène site of Požaha (c. 150-40 BC), however, are worthy of special comment. They come from a different environment and remote area. The fortified site of Požaha (510 m above sea level) lies far away to the NE, to the outside of the "old settlement oikumene", in the foothills of the Moravian-Silesian Beskydy Mts (see Fig. 2). This area is geographically open to the Polish lowlands and forms an important communication corridor via the Moravian Gate.

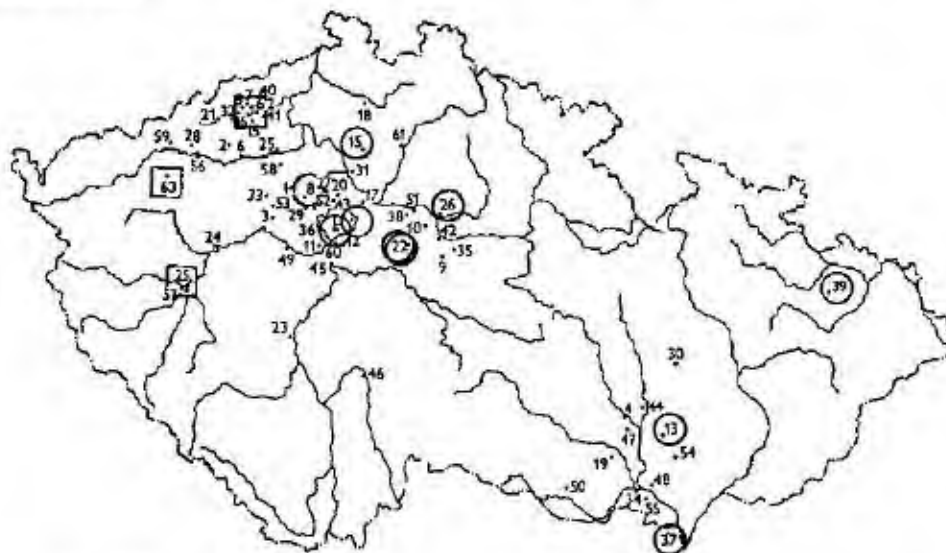


Fig. 2 Map of the Czech Republic with bone samples analysed and published (or in prep.). Sites in boxes contained elk bones (squared - Neolithic, circle - about 1000 BC). Site numbers: 1. Bilina (Teplice district), 2. Blažim (Louny), 3. Bratronice (Kladno), 4. Brno-Bystrc, 5. Břešťany (Teplice), 6. Březno (Louny), 7. Břežánky (Teplice), 8. Budeč (Kladno), 9. Bylany (Kutná Hora), 10. Cerhenice (Kolín), 11. Černošice (Praha-west), 12. Dolní Břežany (Praha-west), 13. Holubice (Vyškov), 14. Hornolka (Stehelčevy) (Kladno), 15. Hradsko (Mělník), 16. Jenišův Újezd (Most), 17. Jenštejn (Prague-east), 19. Jezefany-Maršovice (Znojmo), 20. Klíčany (Prague east), 22. Kouřim - Stará and St. Kliment (Kolín), 23. Kozárovce (Příbram), 24. Krašov (Plzeň-north), 25. Křimice (Plzeň), 26. Labice n/Cidlinou (Nymburk), 27. Libčice n/Vltavou (Prague west), 28. Lužice (Chomutov), 29. Makotřasy (Kladno), 30. Malé Hradisko (Prostějov), 31. Mlékojedy (Mělník), 32. Most (Most), 33. Mšecké Žehrovice (Kladno), 34. Mušov (Břeclav), 35. Nové Dvory (Kutná Hora), 36. Ořech (Prague-west), 37. Pohansko (Břeclav), 38. Pohčany (Nymburk), 39. Požaha - Jičina (Nový Jičín), 40. Prosetice (Teplice), 41. Radovesice (Teplice), 42. Radovesnice (Kolín), 43. Roztoky by Prague (Prague-west), 44. Stránská skála (Brno), 45. Sekanka (Prague-west), 46. Sezimovo Ústí (Tábor), 47. Starý Lískovec (Brno), 48. Šakvice-Štěpničky (Břeclav), 49. Tetín (Beroun), 50. Těšetice-Kyjovice (Znojmo), 51. Třebestovice (Nymburk), 52. Tuchoměřice (Prague-west), 53. Tuchovice (Kladno), 54. Velké Hostěrádky (Břeclav), 55. Věstonice Gate (Břeclav), 56. Víkletice (Chomutov), 57. Vochov (Plzeň), 58. Vraný (Louny), 59. Špičák by Mikulovice (Chomutov), 60. Závist (Prague west), 61. Zvířetice - Bělá (Mladá Boleslav), 62. Kopisty (Most), 63. Chotěbudice (Chomutov), P. PRAGUE - Baba (Prague 6), Běchovice (P. 10), Čimice (P. 8), Horní Počernice (P. 9), Hostivař (P. 10), Hostivice (P. 6), Jiská ul. (P. 1), Kobylisy (P. 8), Malá Ohrada (P. 5), Michle (P. 4), Prague Castle (P. 1), Vyšehrad (P. 3).

The geographical distribution of sites yielding elk material in the Czech Republic is far from regular (Fig. 2). All three Neolithic sites are situated in the western part of Bohemia, despite the fact, that large bone samples of the same period were even analysed from the lowlands of southern Moravia and central Bohemia.

This is in contrast with later evidence, i.e. that dated to between 400-1300 AD, which is scat-

tered throughout the lowlands of the settlement *oikumene*. This may reflect the expected preference of this species for lowland wetlands and it is in accordance with the pattern of the present day migration (Kokeš 1965, Briedermann 1971, Anděra & Kokeš 1978) and development of its range (Andreska 1988). The last evidence in archaeozoological records comes from the 14th century.

Only in a single case was the presence of elk determined on the basis of an antler specimen. This was a ritual offering in a human burial from a site located in central Moravia (Holubice). Antlers from settlement features are always fragmented and thus species determination is often a problem. Antlers provided valuable raw material for the manufacture of tools and their occurrence in samples seems to be under-represented.

An analysis of age structure data does not confirm the presence of very young animals. Only one bone was unfused, i.e. from an individual younger than c. 2.5 years. All other bones were fully fused, representing adult animals, certainly older than two years. One bone represents an individual certainly older than c. 4 years and four teeth (two M3) with medium wear were from adult animals.

Elk remains from adjacent countries (e.g. Poland) were not available for comparison. Data from the southern regions of the former East Germany (Müller 1966) supports the occurrence of elk in the early Middle Ages. In that period, the range of the species probably did not reach the left bank of the Elbe river.

Bridault (1992) has studied the Mesolithic status of elk in Europe (between 10 000 BC to 3000 BC in Scandinavia). She stated that the extension of the range of elk from southern to northern Europe took place during the period of the Allerød climatic amelioration. Elk became very important in the Mesolithic cultures of Scandinavia. Its marked decline there was connected with the process of transition towards closed forests during the Boreal. On Zealand island (east Denmark), elk disappeared at the beginning of the Atlantic period. In areas located to the south of the Baltic sea, in a belt from the Ukraine to England, elk remains were only occasionally found in Pre-Boreal and Boreal deposits. It is supposed that small elk populations survived in certain isolated areas within these regions. Our Neolithic records may represent the presence of such declining populations during the Boreal and Atlantic periods.

Despite the fact that the studied elk remains result from an intentional selection from an unknown area around settlements, archaeozoological material supports the opinion that elk was in some Holocene periods (especially in the case of later evidence, about 1000 AD) a stable member of our fauna. Its occurrence was probably not permanent throughout the Holocene. It is always, of course, a danger to overestimate missing data, especially in the case of very rare events, but it seems that for several thousand years the lowlands were not occupied by this species. The later occurrence of elk has a more similar distribution pattern to those described by Briedermann (op cit. 9) for its modern expansion.

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***Protaphorura unari* sp. n. (Collembola: Onychiuridae) from the Tatra National Park  
(Slovak Republic)**

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Taxonomy, ecology, soil mesofauna, Collembola, Onychiuridae, *Protaphorura unari* sp.n., Slovakia

**Abstract.** A new species of Collembola, *Protaphorura unari* sp.n. from the western part of the Tatra National Park is described. It is a eudominant, euedaphic species in some alpine ecosystems on granite bedrock.

INTRODUCTION

A new eudominant and constant euedaphic species of *Protaphorura* Absolon, 1901 was discovered during long-term ecological studies of alpine, subalpine and mountain forest ecosystems in the western part of the Tatra National Park, Slovak Republic (Rusek 1993). It is herein described.

*Protaphorura unari* sp. n. (Figs 1 - 3)

**DIAGNOSIS.** 1.7 mm long, white. Dorsal pseudocellar formula: 33|023|33342; anapleurite I, II and III and ventral side of head with 1 pseudocella on each side. Chaetotaxy of pronotum i3-, abdominal tergites without chaeta s', 2+2 dorsal microchaetae on abdominal tergite VI in front of anal spines in two parallel rows. Claw without teeth. Both sexes known.

**DESCRIPTION (holotype).** Body 1.7 mm long and 0.5 mm wide. Colour white. Granulation on the whole body relatively fine, most coarse frontally on head dorsum and on lateral parts of meso- and meta-notum, where granules reach 1 - 1.5 µm in diameter. Macrochaetae well differentiated (Figs 1A-D), 65-90 µm long, longest macrochaetae on abdominal tergites V and VI (Figs 3C-D). Sensillae (s) characteristically blunt, slightly thickened and curved, 23-25 µm long, occur among common chaetae (Figs 1A-D). 2+2 of these sensillae occur on the hind part of head (Fig. 1A) and on mesonotum up to abdominal tergite V (Figs 1B-D, 3C). Sensilla s' missing on abdominal tergites. Chaetotaxy of pronotum i3-. Meso- and meta-notum laterally with microsensilla s' in a small pit (Fig. 2C). M:s on abdominal tergite V as 70:23 µm. 2+2 dorsal microchaetae (a1 and p1) in front of anal spines inserted in two parallel rows, unpaired chaeta ko (kx in Pomorski 1990) missing (Fig. 3D).

Chaetotaxy of pro-, meso- and meta-sternum 1,1,2. Pseudocelli circular, 7-8 µm in diameter. Pseudocellar formula: 33|023|33342, anapleurite I, II and III and ventral side of head with one pseudocella on each side.

Antennae with head ratio as 270 : 300 µm. Antennal segment IV (Fig. 2A) with thin sensillae. Antennal organ III (Figs 2A, B) consists of two granulated, slightly curved sensory clubs of equal size (10 µm), two smooth, 6 µm long sensory rods between them, five finger-like protecting papillae and five protecting chaetae. One microsensilla near the base of ventral (fifth) protecting chaeta and another one above it in basal third of antennal segment IV (Fig. 2A).

Postantennal organ (Fig. 3B) 30 µm long and 15 µm wide. It consists of 33 simple vesicles.

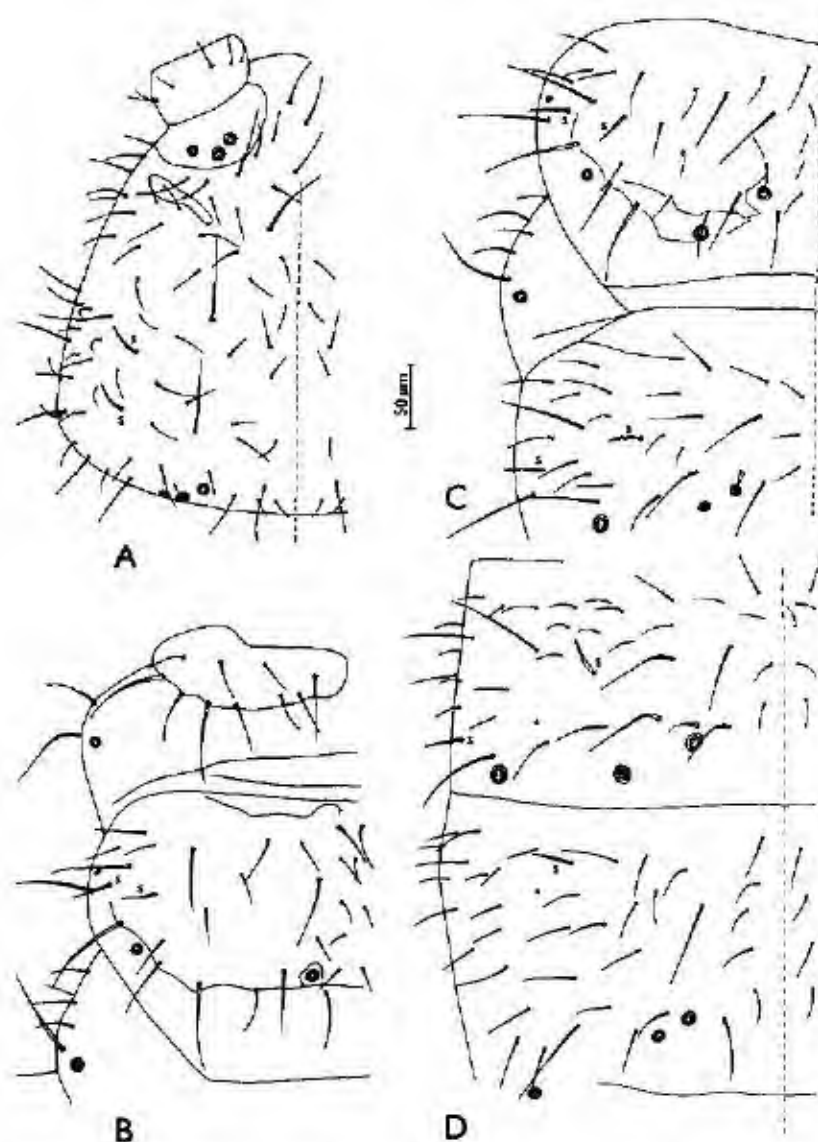


Fig. 1. *Protaphorura unari* sp.n., A - dorsal chaetotaxy of head (left side), B - chaetotaxy of left side of pro- and meso-notum, C - chaetotaxy of left side of meta-notum and abdominal tergite I, D - chaetotaxy of left side of abdominal tergites III-IV. Scale: A-D 50 μm.

Claws 50 μm long, without teeth (Fig. 2D). Empodial appendage 38 μm long, with long bristle and without inner lamella (Fig. 2D). Clavate tibiotarsal tenent hairs missing (Fig. 2D).

Ventral tube with 9 - 10 chaetae on each side. Rest of furca with two microchaetae. Male genital papilla covered with many microchaetae (Fig. 3A). Anal spines 35 μm long and 23 μm in diameter at base (Figs 3A, D).



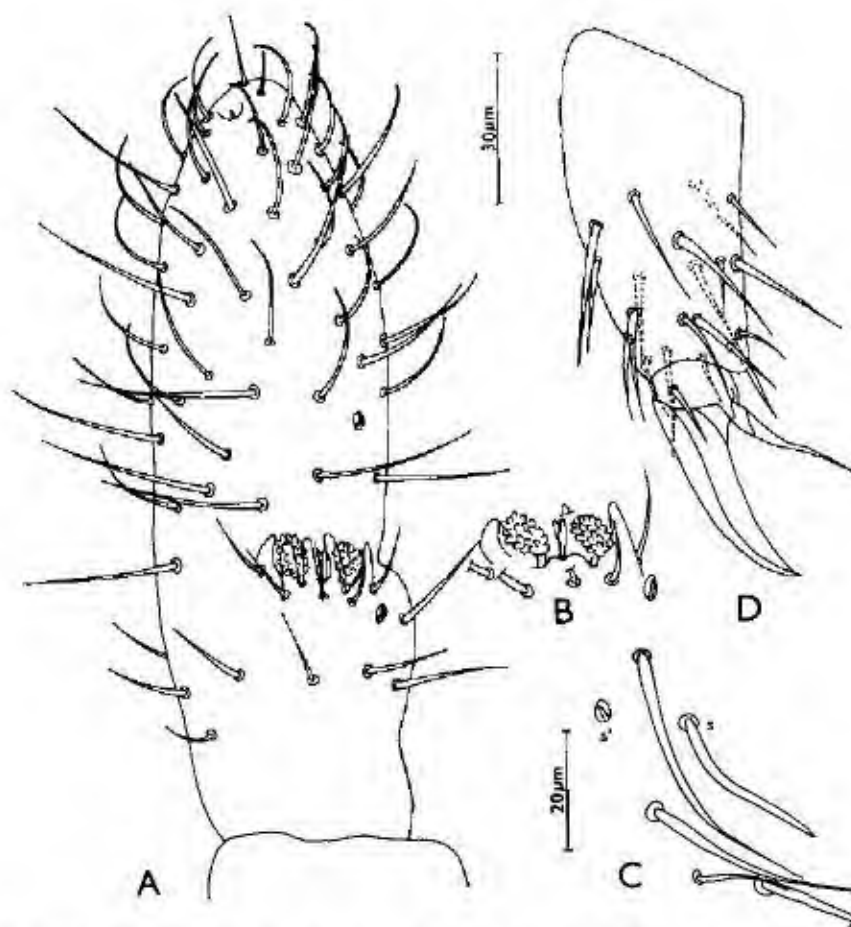


Fig. 2 *Protaphorura unari* sp. n. A - dorsal side of antennal segments III-IV, B - antennal organ III (protecting papillae and chaetae drawn partly), C - chaetotaxy of lateral part of metanotum, D - tibiotarsus and claw III. Scales: A, D 30 µm, B, C, 20 µm

**AFFINITIES.** The new species is related to *Protaphorura subarmata* (Gisin, 1957) and *P. nemorata* (Gisin, 1952). It has the same chaetotaxy of pronotum (i3-), abdominal tergite VI (insertions of 2+2 dorsal microchaetae in front of anal spines forming two parallel lines) and s' missing on abdominal tergites as in *P. subarmata*, but on abdominal tergite V there are 2+2 pseudocelli in the sp. nov. (3+3 in *P. subarmata*). In the case of *P. nemorata* the pseudocellar formula is the same as in the new species, but the chaetotaxy is different. *P. nemorata* bears the m chaeta on pronotum (i3m) and the dorsal microchaetae on abdominal tergite VI in front of anal spines are arranged in two convergent rows.

**HOLOTYPE** female No. 7.7. 1992/B - 44 and 50 paratypes in the author's collection in the Institute of Soil Biology, Academy of Sciences of the Czech Republic, České Budějovice.

**LOCUS TYPICUS.** Slovak Republic, Tatra National Park, Tomanova Dolina Valley, N slope of the Polska Tomanova, Ferečiny, in the western gully, 1760 m ASL, in ecosystem with the plant community *Calamagrostetum villosae* Szaf., Pawl. et Kulcz. 1923, soil type alpine mull-like ranker

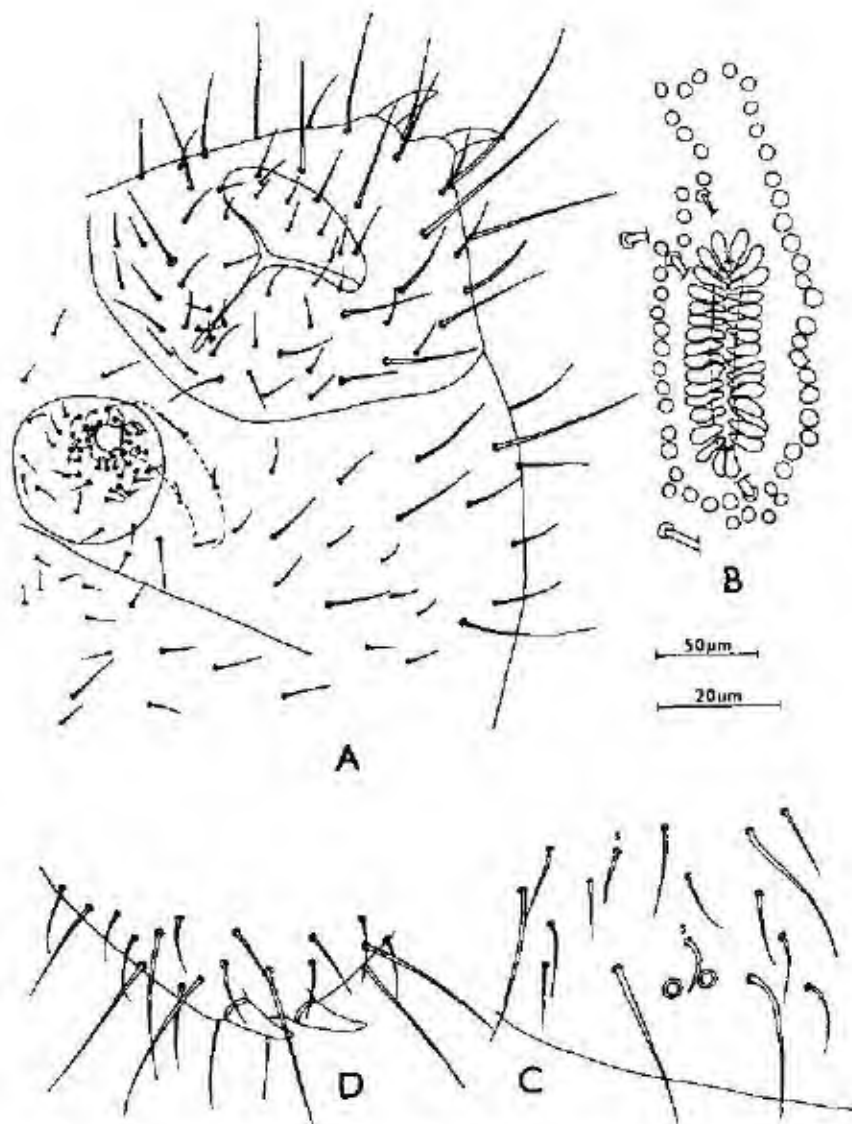


Fig. 3. *Protapharus unari* sp. n., A - ventral chaetotaxy of hind abdominal segments and male genital papilla, B - postantennal organ, C - chaetotaxy around pseudocelli on abdominal tergite V, D - dorsal chaetotaxy of abdominal segment VI. Scales: A, C, D 50 μm, B 20 μm.

on granite, in soil samples, 7.VII.1992 224 specimens, J. Rusek leg.

FURTHER LOCALITIES: - as locus typicus, but east of Tomanove Sedlo Pass, 1592 m ASL., on moist places near swampy remnants of a former alpine lake, in soil samples from the plant community *Hygrocnardetum strictae* (Wall. in Pawl. et al. 1928) Kraj. 1934, 22.VI.1977 80 specimens, 11.VII.1990 16 specimens, 26.IX.1990 21 specimens, J. Rusek leg., - as locus typicus, but east of Tomanove Sedlo Pass, 1593 m ASL., near swampy remnants of a former alpine lake, in soil samples from the plant community *Luzuletum spadicaceae tauricum* (Szafer et al. 1927) Br.-Bl. 1940, 22.VI.1977 434 specimens, 11.VII.1990 one specimen, 26.IX.1990 10 specimens, J. Rusek leg., - as locus typicus, but on the northern

slope of Polska Tomanova, 1660 m ASL, in soil samples from the plant community *Vaccinietum myrtilli subalpinum* (Szaf. et al. 1923) Silb. 1933, 22.Vi.1977 78 specimens, 11.Vii.1990 five specimens, J. Rusek leg.

**DERIVATIO NOMINIS.** The new species is devoted to my friend, plant ecologist Dr Jiří Unar, Masaryk University at Brno. He has studied extensively the plant communities of the Tomanova Dolina Valley where the new species was discovered.

#### A c k n o w l e d g m e n t s

The ecological studies in the Tomanova Dolina Valley were supported by the Granting Agency of the Academy of Sciences of the Czech Republic (grant number 66604). I am obliged to Dr V. G. Marshall, Canadian Forest Service, Victoria, for improving the English of the manuscript.

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The occurrence and biology of *Dasineura gleditschiae*  
(Diptera: Cecidomyiidae) in Serbia

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Received December 5, 1994, accepted February 9, 1995

Published June 22, 1995

Distribution, biology, harmfulness, control, Cecidomyiidae, Diptera, Serbia

**Abstract.** The Nearctic species *Dasineura gleditschiae* (Osten Sacken, 1866) causing galls on the leaflets of *Gleditsia triacanthos* L. is recorded for the first time in Serbia. The biology, harmfulness and control were studied during 1993-1994 in trials in the vicinity of Belgrade. Several overlapping generations have been recorded a year. Considerable damage provoking early defoliation of terminal parts of host plant was recorded and methods of control are discussed.

INTRODUCTION

The honeylocust, *Gleditsia triacanthos* L. (Fabaceae, Leguminosae) is a native of subtropical North America. It was introduced into Europe at the beginning of the 18th century. In Yugoslavia it may often be seen as an ornamental shrub in parks, along paths and in gardens from the Adriatic coast deep into the continental part (inland). It is mostly used to form hedge-rows (Josifović 1972), because of its hard thorns and the fact that it can be cut and has low demands during its growth.

The gall midge species causing the pod-like leaf galls on *Gleditsia triacanthos* was described but very briefly under the name *Cecidomyia gleditschiae* by Osten Sacken in 1866, from the type-locality Newport (R.I., New England, U.S.A.). Very soon *D. gleditschiae* was recorded at many localities in the western parts of the United States (Felt 1915, Barnes 1951).

Gagne (1989) mentioned *D. gleditschiae* in his book about the plant-feeding gall midges of North America and gave figures of a larva, pupa, male and female (total views). He reported that this species may have five to seven generations a year in North America and that the repeated defoliation can cause the death of small branches. According to his information, *D. gleditschiae* is widespread in North America and it was probably spread to the west coast with nursery stock.

Galls of *D. gleditschiae* were found in 1976 in western Europe, in the Netherlands (Nijveldt 1980) and several years later, in 1980, in southern Europe, near Como, northern Italy, in gardens on plants which were imported from the Netherlands (Bolchi-Serini & Volonté 1985). Based on these data, *D. gleditschiae* was included in the Catalogue of the Palearctic Diptera (Skuhravá 1986).

Halstead (1992) reported that this species has also been present in the UK since the early 1980s and has been recorded at a number of localities in southern England.

MATERIAL AND METHODS

The pod-like leaf galls caused by larvae of this gall midge were found at several localities in Serbia, viz. Beograd

(Belgrade), Zemun, Sremski Karlovci, Srebren and Zrenjanin during the years 1993-1994. Malformed leaves from the top branches were sampled to determine the gall maker. The life cycle, harmfulness and possibility of control were studied both in the field and under laboratory conditions.

## RESULTS

The galls on the leaflets of *Gleditsia triacanthos* L. observed in 1993 for the first time in Serbia are induced by the Nearctic species *Dasineura gleditschiae*.

### Morphology

Adults of *D. gleditschiae* are black grayish in colour, males are 1.8-2.1 mm, females 2.2-2.5 mm long, antennae in both sexes 2+12 segmented. Flagellomeres in male with stems, in females without stems; maxillary palps four-segmented. Claws bear a minute tooth at the base; empodium longer than claws. Three vertical gray stripes are located on the dorsal part of the thorax, the

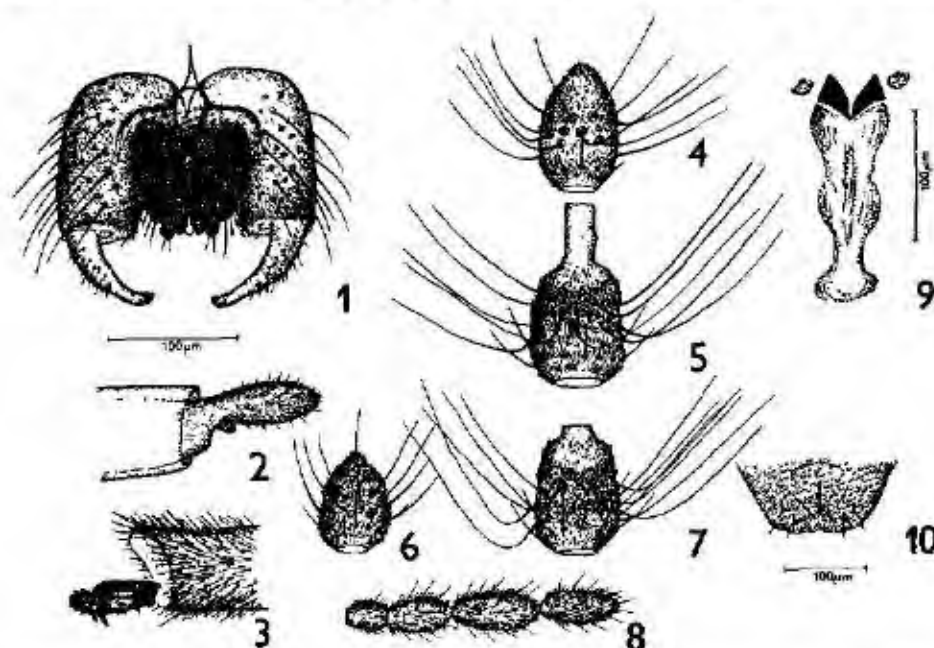


Fig. 1 *Dasineura gleditschiae*, morphological characters of adults (1-8) and of larva (9-11). 1 male terminalia, 2 terminal part of ovipositor; 3 end part of the leg, 4 terminal flagellomere of male, 5 the fifth flagellomere of male; 6 terminal flagellomere of female, 7 the fifth flagellomere of female; 8 maxillary palpus; 9 spatula sternalis; 10 anal segment with terminal papillae

middle one being considerably shorter. A number of large bristles is straggled over the stripes. Horizontal black stripes can be seen on the abdomen which is orange coloured in mature females. Long pale bristles are distinguished on the rear of the tergites. Detailed morphological characters of male and female are given in Fig. 1.

Eggs are red in colour, cylindrical, approximately 0.2 mm in length. The chorion is smooth.

Young hatched larvae are transparent and about 0.3 mm long. Fully grown larvae are white or pale orange in colour and 2.0-2.5 mm long. Their spatula sternalis has a bilobed anterior part on the ventral side of the prothoracic segment. On the anal segment there are four pairs of papillae bearing short setae. Larvae of *D. gleditsiae* have a relatively simple digestive system which is typical of plant-feeding gall midges (see Fig. 2.).

Pupae are dark orange in colour, with black head and alar theca, approximately 2 mm long.

Galls on leaflets of *Gleditsia triacanthos* are pod-like, green to purple in colour and vary in size depending on the age of the attacked leaf (Fig. 2.). Gall length ranges from 4 to 15 mm. The gall mainly comprises a whole leaflet which is folded along the main nerve, with the fissure between the bent parts and numerous hairs shown on a horizontal section of a gall. When the older leaflet is attacked, the gall comprises only a minor part of the leaf surface. Flower- or berry-like galls are formed on the young top leaves attacked.

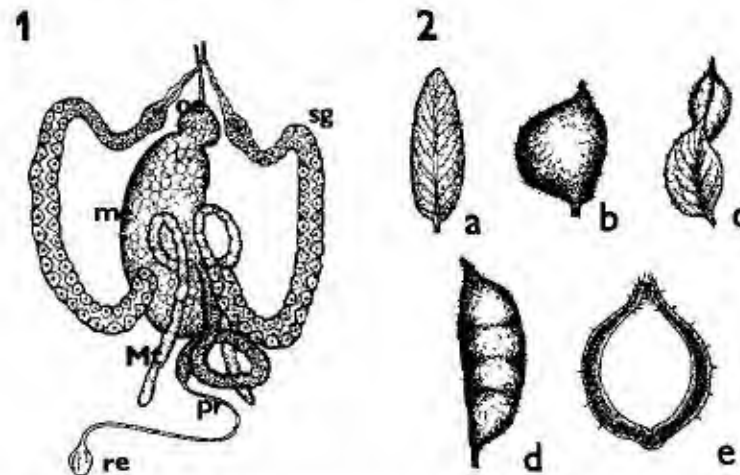


Fig. 2. *Dasineura gleditsiae*: 1 digestive system of larva with large salivary glands (sg) and alimentary canal divided into oesophagus (oe), mesenteron (me), proctodeum (pr), rectum (re), with a pair of Malpighian tubules (MT); 2 galls of various shape (b, c, d) caused by larvae on leaflets of *Gleditsia triacanthos*, in contrast to normal developed leaflet (a); cross-section of one gall (e).

## Biology

Fully grown larvae hibernate in cocoons either in galls that have fallen off or outside, in the surface layer of the soil. First emerged adults were observed in early spring, on the 2nd April, 1994, at Belgrade. Females laid their eggs in large numbers in the middle of April. Adults emerged in the morning with maximum between 7 - 9 a.m. Proterandry was confirmed. In the course of a year the relation of the number of females and males varied. In the population at the beginning the males predominate (2 males : 1 female), later the number changed in favour of females and in autumn the males were rare (1 male : 4 females). Females laid their eggs on the leaf petiole or inserted them on young leaves. Eggs were laid in uneven batches and their number amounted to a couple of hundred per leaf.



The hatched larvae moved towards the edge of the young unopened leaves so the leaves attacked did not open at all. Leaf walls thickened and turned into a pod-like galls. The number of larvae in the galls ranged from one to five, mostly two or three larvae in one gall were observed. Larvae were arranged next to each other in separate depressions in the gall wall. Sometimes a cobweb-like screen was noticed between larvae.

In most cases pupation takes place in the galls. Prior to eclosion the pupae moved to the edge of the gall and sometimes one half of their body was sticking out from the opening of the gall. Exuviae of pupae were commonly seen upon the galls for some time. A smaller part of fully grown larvae leave galls during the growing season and drop to the soil where they hibernate in the upper surface.

Both white and orange coloured larvae occur in galls but seem to be identical from the morphological point of view. Whitish larvae predominated in populations until the middle of the growing period and orange coloured larvae were numerous from mid-summer onwards. Probably the changes in the colouration may be connected with biochemical processes in host plant tissues at the beginning of autumn.

Egg development lasts 3 to 4 days, larval development 10 to 14 days and the pupal stage 17 to 25 days. Total development of one generation may last usually 17 to 25 days but up to 43 days. *D. gleditchiae* has several overlapping, insufficiently distinctly separated generations a year in Serbia. All stages (adults, eggs, larvae, pupae) may occur at the same time during one growing season from April up to November. In 1993 the last emerged adult was recorded at the beginning of November. At lower temperatures the larvae have been observed to spin a dense cobweb coat in the gall before hibernation. During the year a number of larvae leave galls and produce fine cocoons in the upper surface layers of the soil and hibernate there. No emergence of adults was recorded from larvae which had left galls during 1993 and 1994. These larvae were, however, still alive. This confirms the polymodal development of *D. gleditchiae*.

### Harmfulness

The leaflets of *Gleditsia triacanthos* which had been attacked by larvae of *D. gleditchiae* turn into pod-like formations, the galls, which are variously coloured from green to purple. After larvae have finished feeding, the leaflets die and fall off. Heavy attack causes mostly leafless top branches and results in considerable damage. There is no doubt that the early defoliation affects all life processes of attacked plants. Such plants lose their decorative purpose. However, damage is compensated for with progressive growth of plants which form new leaves.

As a control measure we suggest cutting and burning of attacked branches of honeylocust which is environmentally friendly regardful.

### Distribution

*Dasineura gleditchiae* is a native Nearctic species widespread in North America. It has been introduced into Europe probably by transmission with small green plants (nursery stocks). Galls of *D. gleditchiae* were first observed in Europe in 1976 in the Netherlands, in 1980 in northern Italy and in the 1980s in England.

*D. gleditchiae* was recorded in several localities in Serbia during 1993-1994. It is the fourth country occurrence in Europe. In June 1994, *D. gleditchiae* caused considerable damages on honeylocust in Zemun, Serbia. Most top branches were quite without leaflets.

At present, *D. gleditchiae* occupies a large distribution area in North America between 30 to 45 degrees of the northern latitude, and in Europe between 40 to 50 degrees of the northern lati-

tude (Fig. 3.). From the point of view of composition of fauna, *D. gleditchiae* is an introduced species of the gall midge fauna of the Palearctic Region.

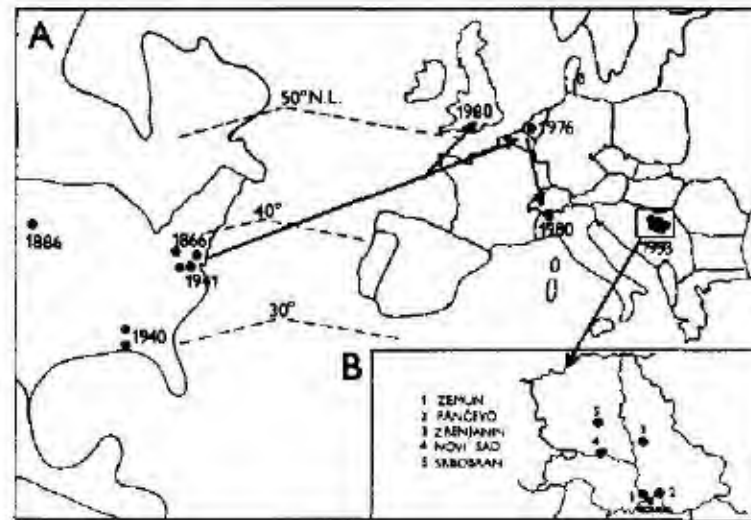


Fig. 3. The native distribution of *Dasineura gleditchiae* in North America and its occurrence in several countries of Europe (A); detailed occurrence in Serbia during period 1993-1994 (B).

#### SUMMARY

The Nearctic gall midge species *Dasineura gleditchiae* causing galls on the leaflets of *Gleditchia triacanthos* was recorded for the first time in Serbia. It is the fourth country record in Europe. The short description of morphological characters of adults, eggs, larvae and pupae together with descriptions of galls is given. The biology, harmfulness and control were studied during 1993-1994 in trials in the vicinity of Belgrade. The embryonic development in eggs lasts 3-4, larval development 10-14 and pupal stage 17-25 days.

Total development lasts mostly 17-25 days but up to 43 days. Several overlapping generations develop a year. Considerable damage causing early defoliation of terminal parts of the host plant were recorded which has a negative affect on all life processes and reduces the decorative purpose of this ornamental shrub. The best measure against this pest is cutting and burning attacked branches. *D. gleditchiae* is a native Nearctic species which was accidentally introduced into Europe, probably with small young plants (nursery stocks).

#### Acknowledgements

We wish to thank to Dr K. M. Harris (Ripley, Woking, Surrey, UK) for his advice and for critical reading and comments to the manuscript.

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## Fecundity of Pikeperch (*Stizostedion lucioperca*) in two Bulgarian reservoirs as compared to other European habitats

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Received September 6, 1993, accepted February 9, 1995

Published June 22, 1995

Ecology, fecundity, water reservoirs, *Stizostedion lucioperca*, Bulgaria

**Abstract.** In this study we critically survey the methods of comparative studies of fish fecundity which have been most often used in studies described in East-European literature. We suggest a way which is more precise and suitable for this purpose (exemplified by an example of 10 populations of pikeperch covering their natural range), and, on this basis, we try to reveal certain peculiarities and regularities in the interpopulation variation in pikeperch fecundity.

### INTRODUCTION

No data on the reproductive biology of pikeperch in the water bodies of Bulgaria are available in the literature form, as they are too scarce for the entire Balkan Peninsula. The main studies were carried out in two reservoirs which differ strongly in ecological characteristics. The obtained results were compared with similar ones from other water bodies.

### MATERIAL AND METHODS

The material was collected from Ovčantsa Dam (South Bulgaria) and Batak Dam (the Rhodopes). Ovčantsa Dam is a cooling reservoir of a thermo-electric power station. Water is pumped from the reservoir to cool the turbines, and then returned to the reservoir. The reservoir is at an altitude of 170 m, has an area of 600 ha, and an average depth of 5 - 6 m. The mean annual temperature is 16.2°C. Mean monthly values for January and August are 6.3°C and 25.6°C, respectively. Batak Dam is a mountain reservoir (1100 m alt.) with an area of 2 107 ha, an average depth of 14.5 m, a mean annual temperature of 13.3°C, and mean monthly temperatures for January and August of 1°C, and 19.8°C, respectively.

The material was collected during the period from 1981 to 1986. The standard length (L) and weight (G) of fish without their viscera, were measured. The age was determined from scales. The absolute individual fecundity (i.e., the number of ready-to-spawn eggs in one individual) was determined gravimetrically. For this purpose, the material was collected in February-March (from Batak Dam - to April) when fish gonads were in their final, fifth stage of maturity (according to the Nikolskiy (1974) scale). The average absolute fecundity ( $\bar{F}$ ) (i.e., the average number of eggs from individuals of a certain size, weight, or age group (Brylinska and Brylinsky 1974, Spanovskaja and Grigorov, 1976), was used for the correlation-regression analysis of the relationships between fecundity, length and weight, of pikeperch. For choosing the most appropriate functions to describe these relationships, their dispersions were used ( $D = \sum (F_i - \bar{F})^2$ , where  $F_i$  are the theoretically calculated average values of fecundity, and  $\bar{F}$  - are their corresponding empirical values (Sepetlieva, 1968). This analysis was also accompanied by values for the coefficient of determination ( $R^2$ ).

Relative fecundity (RF) was computed as an index  $\bar{F}/G$  (Spanovskaja, 1976). Their coefficient  $b$  (or  $b$  in %) from the equation  $F = a + bG$  was also used as a relative fecundity (Zotin, 1961, 1968, Živkov, 1983). The Ivlev (1953) model

$(PF = k \sum p f \sum [t_p(t - m)] / 100 \sum p t)$ , was used in studying population fecundity. In this model,  $k$  is the number of spawnings per annum,  $t$  is age in years,  $t'$  is the age of maturity,  $t''$  is the age at which reproduction ceases (this was the maximum age of the fish collected),  $p$  is the relative number of individuals of each age-group (in %),  $f$  is the relative

number of females in age-group (in %),  $F$  is the average absolute fecundity for each age group, and  $m$  is the relative number of males in each age group.

The index of relative population fecundity, was determined through the Nikolskoy (1974) method.  $PF$  = average fecundity of one female/average age of one female, i.e. the average fecundity of 1 (100, 1000) female (s) with a particular age structure of the spawning population.

Population reproduction rate ( $V_p$ ), i.e. the number of females created by one mature female for a period of one year, was determined by the Poljakov (1971) method.  $V_p = \sum V_i P_i / 100$ , where  $V_i = 1/SF_i$  is the average parameter of the reproduction of a female which spawns for the first time at the age of  $i$ , and has absolute average fecundity  $F$  eggs.  $S$  is the percentage of females in a population,  $i'$  is the year of the first spawning of the females which have matured earliest,  $i''$  is the year of the first spawning of the females which have matured last,  $P_i$  is the percentage of females which spawn for the first time at the age of  $i$ . Published empirical data on eight other water bodies were used for comparison, and for the correlation and regression analysis of the increase of pikeperch fecundity with length and weight. These water bodies were: Verhne-Uralskoe Reservoir, Russia (Perminov 1975), the Gulf of Finland (Ilenkova, 1974), the Gulf of Kourskya-Mares, Lithuania (Virbickas et al., 1974), the Delta of the Danube (Kukuradze, 1965), Orava Dam, Slovakia (Bastl, 1970), Tsimlyanskoe Reservoir, Ukraine (Koval, 1980), Lake Ilmen, Russia (Fyodorova, 1975), and Gorkovskoe Reservoir, Russia (Turanova, 1970).

Table 1. Changes of absolute fecundity in different length classes of pikeperch in Batak Dam, N - number of fish

Length class, mm	Average length (L), mm	Absolute fecundity F, M eggs		N
		Range	Average	
281 - 320	308	26 890 - 83 290	47 290	3
321 - 340	335	30 238 - 54 828	46 630	4
341 - 360	352	25 669 - 143 207	95 909	9
361 - 380	371	105 870 - 185 344	134 799	5
381 - 420	409	210 891 - 271 296	231 405	3
421 - 440	432	233 290 - 305 993	275 031	4
441 - 480	465	284 391 - 615 799	430 308	4
481 - 500	496	319 292 - 585 860	478 432	6
501 - 520	512	406 456 - 746 011	522 077	9
521 - 540	531	488 347 - 850 532	652 154	10
541 - 560	549	651 053 - 687 838	666 846	3
661 - 700	682	1 187 626 - 1 340 477	1 264 052	2

## RESULTS

### 1. Absolute fecundity

The absolute fecundity of pikeperch in Batak Dam, varies from 25,669 up to 1, 340, 477 eggs (Table 1), with minimum and maximum sizes, weights, and ages 308 mm, 275 g, 2 years and 685 mm, 4, 350 g, 6 years, respectively. The weighted average fecundity of the whole populations, was 404, 376 eggs. The absolute fecundity of pikeperch in the cooling reservoir of Ovčaritsa, varies from 18, 392 up to 2, 100, 526 eggs (Table 2), with minimum and maximum sizes, weights, and ages 284 mm, 232 g, 1 year and 778 mm, 6, 420 g, 5 years, respectively. The average fecundity is 420, 430 eggs.

Table 2 Changes of absolute fecundity in different length classes of pikeperch in Ovčariša Dam, N - number of fish

Length class, mm	Average length (L), mm	Absolute fecundity F, M eggs		N
		Range	Average	
281 - 360	340	18 392 - 101 528	100 946	3
361 - 380	372	41 409 - 129 032	83 741	3
381 - 420	403	146 829 - 197 883	172 221	3
421 - 440	431	130 608 - 281 098	202 828	4
441 - 460	454	164 680 - 272 327	208 796	3
461 - 480	469	177 03 - 460 931	266 845	8
481 - 500	492	240 69 - 476 97	358 832	2
501 - 520	513	121 471 - 638 195	385 224	3
521 - 540	532	233 560 - 261 419	245 872	3
541 - 560	549	219 045 - 630 090	424 568	2
561 - 580	573	231 228 - 756 125	579 208	4
581 - 600	588	261 419 - 862 905	564 398	5
641 - 680	660	529 116 - 990 513	759 814	2
681 - 780	734	1 039 738 - 2 100 526	1 570 132	2

## 2. Relative Fecundity

The relative fecundity, (RF) calculated as a number of eggs (F) per 1 kg of the female's weight (G), i.e. as a ratio of F and G, for the populations investigated, is characterized by considerable individual variability. The average values of RF, also vary, in the different weight classes (Tables 3 and 4). Nevertheless, the tables show that RF's average values also increase with average weight. The average value of relative fecundity for Batak Dam (268) is higher than the one for Ovčariša Dam (195).

Analogous results are obtained, if the coefficient b in the equation  $F = a + bG$  is used as a para-

Table 3 Changes of the absolute and relative fecundity in different weight classes of pikeperch in Batak Dam, N - number of fish

Weight class, g	Average weight, (G), g	Average absolute fecundity (F), M eggs	Relative fecundity (F/G), eggs	N
201 - 400	338	45 987	136	6
401 - 600	531	92 447	174	7
601 - 800	668	117 816	176	8
801 - 1000	916	265 025	289	8
1001 - 1400	1260	489 135	388	3
1401 - 1600	1478	484 971	328	5
1601 - 1800	1703	579 904	340	7
1801 - 2000	1989	633 798	334	12
2001 - 2200	2170	721 077	332	3
3201 - 4400	406	1 264 052	311	2



Table 4. Changes of the absolute and relative fecundity in different weight classes of pikeperch in Ovčaritsa Dam. N - number of fish

Weight class, g	Average weight, (G), g	Average absolute fecundity (F), M eggs	Relative fecundity (F/G), eggs	N
201 - 600	474	87.329	184	4
601 - 1000	694	110.243	159	4
1001 - 1200	1145	223.461	195	4
1201 - 1400	1321	240.770	182	7
1401 - 2000	1717	260.536	152	3
2001 - 2200	2135	226.302	106	2
2201 - 2400	2322	543.241	234	3
2401 - 2600	2500	440.796	176	2
2601 - 2800	2697	772.462	286	3
2801 - 3000	2970	659.833	222	3
3001 - 3600	3275	604.116	184	2
4601 - 4800	4650	1 015.126	218	2
6401 - 6600	6420	2 100.526	327	1

Table 5. Changes of the regression parameters in the equation  $F = a + bG$  for the relationships between the average absolute fecundity (F) and average weight (G) of females without their internal organs, for different populations of pikeperch. N - number of fish, r - correlation coefficient

Water body	a	b x 100	r between F and G	N
Verhne-Uralskoe Reservoir (Russia)	-113.68	27.12	0.95	74
the Gulf of Finland	-100.96	35.59	0.98	124
the Danube Delta	-37.83	21.32	0.98	64
Batak Dam (Bulgaria)	-35.20	33.60	0.99	62
Gorkovskoe Reservoir (Russia)	-23.03	18.23	0.98	86
Ovčaritsa Dam (Bulgaria)	-21.92	31.36	0.95	46
the Gulf of Kurshyu-Mares (Lithuania)	-15.27	25.05	0.94	74
Lake Ilmen (Russia)	-12.64	15.01	0.99	82
Orava Dam (Slovakia)	-3.03	17.30	0.98	30
Tsimlyanskoe Reservoir (Ukraine)	13.81	14.77	0.99	292

meter of relative fecundity (Table 5). The value of b, for Ovčaritsa Dam, is 0.3136, and for Batak Dam - it is 0.3360. This means that as females' weights increase with 1 g as an average, their fecundity increases with an average of 314 eggs, for the first water body, and with 336 eggs, for the second one.

### 3. Population Fecundity

Population fecundity (PF) is most often calculated by using the formulas of Ivlev (1953), Nikolskiy (1974), and Poljakov (1971). For this it is necessary to know a number of biological

Table 6 Biological parameters and population fecundity (PF) of pikeperch in two Bulgarian reservoirs

Water body	Females in the population, %	Average absolute fecundity, eggs	Average age of the fish, years	Females at first maturity in a particular age-group, %			PF, calculated through different models		
				1	2	3	Ivlev (1953)	Nikolsky (1974)	Polyakov (1971)
Batak Dam	55.2	404,376	3.88		28.6	71.4	57,530	104,221	96.6
Ovčaritsa Dam	31.7	420,430	2.45	10.3	89.7		54,398	171,604	7,320

parameters for the particular populations, (Table 6). The average absolute fecundity of pikeperch in Ovčaritsa Dam (420, 430 eggs) is slightly higher than in Batak Dam (404, 376 eggs). The population fecundity in Batak Dam, calculated using the Ivlev formula, is slightly higher (57, 398 eggs) than in Ovčaritsa Dam (54, 398 eggs). The reason for this is that in the latter dam, the percentage of females was lower (31.7) than in Batak Dam (55.2).

The results obtained from the Nikolsky (1974) formula, were just the opposite. PF was 171, 604 eggs for Ovčaritsa Dam, and 104, 221 eggs for Batak Dam, because the average age of the population in the latter water body, was higher (3.88 years) than the age in the former (2.45 years) (Table 6). The parameter of population reproduction rate ( $V_p$ ), after Polyakov (1971), i.e., the number of females created by one mature female for a period of one year, was 70 times higher for Ovčaritsa Dam (7, 320 females) than the value for Batak Dam (97 females), because the females in the first reservoir mature about one year earlier.

Table 7 Predicted absolute average fecundity ( $F$ , M eggs) of pikeperch over range of lengths ( $L$ , mm) in different water bodies.  $r$  - correlation coefficient

Water body	F/L relationship	$r$	Body length, mm					
			300	400	500	600	700	800
Batak Dam (Bulgaria)	$F = 1500/(1+10)$	0.99	47	167	493	985	1323	
the Gulf of Finland	$F = 884.6682 + 2.77L$	0.96	223	499	776			
the Gulf of Korshun-Mares (Lithuania)	$F = 541.8333 + 2.0056L$	0.99	60	260	461	662		
the Danube Delta	$\log F = -11.9102 + 5.3872 \log L$	0.97	27	128	426			
Ovčaritsa Dam (Bulgaria)	$\log F = 3.9562 + 0.0035L$	0.99	74	148	298	599	1204	2422
Verhne-Uralskoe Reservoir (Russia)	$\log F = -5.6712 + 3.0746 \log L$	0.98	88	213	427	742	1192	
Gorkovskoe Reservoir (Russia)	$\log F = 1.4916 + 0.00204L$	0.96	127	203	325	520	831	1329
Tsimlyanskoe Reservoir (Ukraine)	$F = 2100/(1+10)$	0.99	75	150	288	521	853	1231
Orava Dam (Slovakia)	$F = 1200/(1+10)$	0.99	57	139	307	568	842	
Lake Ilmen (Russia)	$F = 370/(1+10)$	0.99	40	129	260	338		

Table 8. Predicted absolute average fecundity ( $F$ , M. eggs) of pikeperch over range of weights ( $G$ , g) in different water bodies.  $r$  - correlation coefficient

Water body	$F/G$ relationship		Weight, g				
			500	800	1000	2000	4000
the Gulf of Finland	$F = -100.962 + 0.3559G$	0.98	77	184	255	611	1323
Batak Dam (Bulgaria)	$F = -35.1961 + 0.336G$	0.99	133	234	301	637	1308
Ovcharitsa Dam (Bulgaria)	$F = 72.5 + 0.07G + 0.0004G^2$	0.98	148	202	242	487	1200
the Gulf of Kurshyu-Mares (Lithuania)	$F = -15.267 + 0.2505G$	0.94	110	185	235	486	987
Verhne-Uralskoe Reservoir (Russia)	$\log F = 2.1471 + 0.0002G$	0.99	178	204	225	359	919
the Danube Delta	$F = -37.8266 + 0.2132G$	0.98	67	133	175	389	815
Orava Dam (Slovakia)	$F = -3.0299 + 0.173G$	0.98	84	135	170	343	689
Gorkovskoe Reservoir (Russia)	$F = 2000 / (1 + 10G)$	0.99	167	190	206	308	628
Tsimlyanskoe Reservoir (Ukraine)	$F = -13.8133 + 0.1476G$	0.99	88	132	161	309	604
Lake Ilmen (Russia)	$F = -12.6411 + 0.1501G$	0.99	62	107	138	288	588

## DISCUSSION

### 1. Absolute Fecundity

Information on pikeperch fecundity in the literature form varies, and is sometimes contradictory. Thus, for example, the minimum individual absolute fecundity ( $F_{min}$ ) of pikeperch in the Lower Dnieper is 180, 500 eggs (Poltavchuk, 1965), while for the Delta of the Danube, where pikeperch mature earlier and at lower sizes and weights,  $F_{min}$  is only 12, 915 eggs (Kukuradze, 1965). The value of the minimum absolute fecundity of pikeperch in Ovcharitsa Dam (18, 392 eggs) is close to the value for the Danube. Batak Dam is among the water bodies for which the values of  $F_{min}$  (25, 669 eggs) vary from 20, 000 up to 26, 000 eggs. These are: Lake Byeloye - 21, 700 eggs (Serenko, 1980); Verhne-Uralskoe Reservoir - 23, 500 eggs (Perminov, 1975), and the Gulf of Kourshyu-Mares - 24, 000 eggs (Virbickas et al., 1974). The minimum fecundity of pikeperch in Lake Ilmen and Tsimlyanskoe Reservoir is higher, 48, 100 eggs (Pyodorova, 1975) and 49, 500 eggs (Koval, 1980) respectively.  $F$  amounts to 95, 400 eggs for Irklinskoe Reservoir (Matyuhin, 1968). The highest values of  $F_{min}$ , have been reported by Poltavchuk (1965) for the Middle and Lower Dnieper (128, 000, and 180, 500 eggs, resp.) and by Oliva et al. (1968) - 200, 000 eggs.

Generally, the maximum individual absolute fecundity of pikeperch ( $F_{max}$ ) is reported to be a million eggs (Zashev, 1961; Oliva et al. 1968). This value has apparently been taken from Berg (1949) who suggested that  $F_{max}$  was 900, 000 eggs. The data on the water bodies studied revealed that  $F_{max}$  values often fall between 500, 000 and one million eggs, i.e. 517, 000 for Middle Volga (Virbickas et al., 1974), 637, 025 for the delta of the Danube (Kukuradze, 1965), 781, 000 for the Caspian Sea (Virbickas et al., 1983), and 899, 600 for the Lower Dnieper (Poltavchuk, 1965). However, for a number of water bodies, these values are higher than 1 million eggs, i.e. 1, 755, 000

eggs for Irlikinskoe Reservoir (Maryuhin, 1968), 1, 109, 000 eggs for the Gulf of Kourshyu-Mares, 1, 129, 000 eggs for the water bodies of Ukraine, 1, 228, 000 eggs for the Kuban River (Virbickas et al., 1974), 1, 340, 500 for Batak Dam, 1, 411, 800 eggs for Tsimlyanskoe Reservoir (Koval, 1980), 1, 550, 000 eggs for Verhne-Uralskoe Reservoir (Perminov, 1975), and 1, 677, 000 eggs for Lake Byeloye (Serenko, 1980). The latter value of  $F_{max}$  is the highest reported in literature. It refers to an individual with a length of 745 mm, and a weight of 7, 240 g (6, 240 without the internal organs), at the age of 16. Only the pikeperch in Ovčarița Dam had a higher maximum absolute fecundity (2, 100, 500 eggs). It was found in an individual that was longer (778 mm) and heavier (6 420 g without the internal organs), but considerably younger (5 years old). Given that under natural conditions, pikeperch reach even bigger sizes, it is clear that their maximum fecundity may considerably exceed even 2 million eggs.

The absolute fecundity of different length, weight, and age classes of a particular population, is most often estimated to allow comparisons with values for other populations. These comparisons, however, are often hampered because many of these classes are not represented in all of the populations being compared. In some populations, minimum fecundity is lower, because the fish mature earlier and at smaller sizes. In other populations, the maximum number of eggs is higher, because there are larger individuals. The average fecundity of a population, which is also used in comparisons, is determined, to a large extent, by these circumstances. The average values of fecundity, for the same size classes in different populations, are also unsuitable for comparison, but they are most often used by various authors who subjectively determine the ranges of the size classes, e.g. with intervals of 10, 20, ... 50 etc. mm. The analogous comparison of fecundity values for the same age-groups, is also useless because the number of eggs for these groups depends mainly on the lengths and weights of fish, which vary at the same age, in different water bodies. The number of eggs in 1 g of ovary, is also unsuitable for comparison, because its value is not a constant which depends on the level of maturity (the weight) of the ovary. The number of eggs related to 1 kg of the female's weight is also unsuitable, because the absolute fecundity/fish weight ratio changes with the increase of the weight (Živkov, 1983).

Because of these difficulties, the comparative analysis of the fecundity of pikeperch in different populations was made in the following way, we found the most suitable equation describing the relationship between the average values of  $F$  and  $L$ ; then we gave rounded values of  $L$  (300, 400 etc. mm) (selected at random), thus calculating the corresponding values of  $F$ . We compared these values of  $F$  for different populations while using one and the same value of  $L$  (Table 7). The populations in Table 7, are presented in the descending order according to the number of eggs in the biggest (last) size class (in case of two populations with different maximum lengths, the comparison of  $F$  values for both of them, was made with respect to the last size class of the population with smaller size). The table suggests several conclusions:

1. There are large differences in the values of the fecundity of pikeperch in different water bodies. Fecundity is higher for the mountain reservoir of Batak and the Gulf of Finland than it is for Orava Dam (Slovakia) and Tsimlyanskoe Reservoir (Ukraine). The rest of the data did not reveal a relationship between water body's geographical position and the fecundity of pikeperch (the lowest fecundity was reported for Lake Ilmen, north of the Orava Dam (Slovakia) and Tsimlyanskoe Reservoir (Ukraine)).

2. There is an obvious tendency for populations of lower initial fecundity (with  $L = 300$  mm) to have higher values of  $F$ , in the next size classes, and vice versa (compare, for example, the populations of the delta of the Danube with those of Verhne-Uralskoe Reservoir, or the one of Batak Dam with the one of the Gulf of Kourshyu-Mares or Gorkovskoe Reservoir).

3. The absolute fecundity of the populations in the cooling reservoir is lower than in Batak Dam (except for the initial fecundity, with  $L = 300$  mm). However, all the other biological characteristics (i.e. growth rate, age at first maturity, condition etc.) of the pikeperch of the cooling

reservoir are better. Apparently, this is one of the negative effects of heated water on the biology of cold-tolerant pikeperch. Similar results on other species living in cooling reservoirs of Lithuania, have been obtained by Virbickas et al. (1983).

We considered that using the average values of absolute fecundity of fish, with equal, round values of their weights without the inner organs (i.e. 500, 1,000, 1,500, etc. g) for comparative studies of the fecundity of different populations (Table 7), should be even better because with the same average length or age of the fish, the corresponding average weights for the different populations, are different (because of their different condition, and growth rate). In other words, the dependence of fish fecundity on fish size and age is determined by the weight at these particular sizes and ages.

## 2. Relative Fecundity

After analyzing the nature of the changes in the classical factor of relative fecundity, i.e. the ratio of fecundity ( $F$ ) and the weight ( $G$ ) of females (the  $F/G$  index), we came (Živkov, 1983) to the conclusion that these changes had nothing to do with the real rate of fecundity increase with female weight. We found that the  $F/G$  index increased or decreased with the increase of weight, depending of whether the regression line  $F - G$  passed under or above the origin. The position of the point at which this line crosses the  $F$  axis, however, depends not only on the line's slope (the coefficient  $b$  in the equation  $F = a + bG$ ) but also on the biological (especially the specific) peculiarity of the  $F/G$  ratio; on females' first maturity, and on the value of the absolute fecundity of the fish which spawn for the first time. That is why we recommend and use the coefficient  $b$  in the equation  $F = a + bG$ , as a parameter of relative fecundity. In most of the cases, this equation describes the  $F/G$  relationship, with a satisfactory statistical precision. The coefficient  $a$ , was provisionally called "initial" or "start fecundity". As the values of the coefficient  $a$  increased from -113.68 up to 13.81, for the 10 populations which we compared, the coefficient  $b$  decreased from 35.59 down to 14.77 (Table 5). A considerable, negative correlation between  $a$  and  $b$  ( $r = -0.67$ ,  $p = 0.05$ ), was found. Our attention was drawn to the presence of such a correlation in the noncarnivorous fish species of Batak Dam, for the first time, in 1983 (Živkov, 1983). In connection with the discussion reflected in the Russian literature (Zotin, 1961, 1968; Nikolskiy, 1974; Spanovskaja, 1976), on the adaptive nature of the changes of fish fecundity and on the relative parameters of fecundity, we reported that the increase of absolute fecundity with the increase of fish weight was a feature which had been encoded in fish genome and which had always been demonstrated within the whole range of environmental conditions under which a population might grow and develop. The rate of this increase will be different in different populations and conditions. It is dependent not only on endogenous, but also on environmental factors. The negative correlation between the absolute fecundity in the earliest years, and the rate of its increase with the weight in the next years, is considered by us as a natural process of regulation of fecundity, depending on the changing environmental conditions.

## 3. Population Fecundity

Ichthyologists often try to estimate, in quantitative terms, the importance of the absolute fecundity, age at first maturity, sex ratio, age structure of the spawning population, as well as periodicity of spawning, etc., for the reproduction of fish. These attempts have resulted in a number of indexes which characterize the fecundity of a species or of its populations. In a survey and a critical analysis of the different indexes (Živkov and Petrova, 1983), we concluded that the popu-



lation parameter ( $V_p$ ), of Poljakov (1971), i.e. the number of females which have been created by one mature female, over one year, is more useful, with respect to both theory and practice, than other parameters of population fecundity (PF) which have been described so far in East-European literature. It enables a quantitative estimation while considering the fact that a change in age of first maturity affects the reproductive capacity of the population more intensively than the changes in fecundity do. This has been illustrated on Table 6. We can see that while 10.3% of the females in the cooling reservoir of Ovčaritsa spawn as early as their first year, and 89.7% of them in their second, there are no mature females in the first year in Batak Dam. In the second year they amount only to 28.6%, and not before the third year do 71.4% of the females spawn. For this reason, the value of  $V_p$  for Batak Dam, is only 97, and for Ovčaritsa Dam - it is 7, 320 females, although the values of the average absolute fecundity of both of the populations are almost equal - 404, 376 and 420, 430 eggs, respectively.

#### SUMMARY

Absolute fecundity ( $F'$ ) of pikeperch in the different water bodies varied between 12, 950 and 2, 100, 500 eggs. No regular relation between  $F$  and the geographical position of the water bodies was found. Pikeperch fecundity in the cooling reservoir Ovčaritsa was lower than the fecundity in the mountain Batak Dam, in spite of the fact that all the other biological characteristics of pikeperch in the cooling reservoir were better. This is assumed to be because of the negative influence of heated water on the biology of this coldtolerant species. The average values of the absolute fecundity ( $F$ ) of the fish of the same weight ( $G$ ) (without the internal organs) was calculated for different populations from their equations for the  $F/G$  relationship. This is the most accurate way of carrying out comparative studies of the absolute fecundity of fish of different populations. The coefficient  $b$  (or  $b$  in %) from the equation  $F=a+bG$ , is recommended as a parameter of a population's relative fecundity. A negative correlation between the so-called "start fecundity" (the coefficient  $a$ ) and the relative fecundity (the coefficient  $b$ ), was found. This phenomenon is considered to be a natural process of the regulation of fecundity, resulting from the interaction between inner (genetic) and environmental factors. Use of the Poljakov (1971) parameter of population reproduction rate is recommended among the parameters of population fecundity, which have been most often described in the East-European literature, so far. It can be used in estimating the potentially possible population reproduction rate, and notes that changes in age of first maturity affect the population's reproductive capacity much more intensively than changes in fecundity.

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**IN MEMORIAM PROFESSOR RNDr. JAN LELLÁK CSc.  
(16. 1. 1926 - 31. 7. 1993)**

During the summer of 1993, all Czech and Slovak limnologists were shocked by the unexpected and sad news of Prof. Lellák's passing away. He was a respected and well known member of our scientific community. Born in the small Slovak village of Hefčmanovce, he moved quite early to the town České Budějovice and in 1947 finished there his secondary education. In the same year, he was accepted to the Faculty of Science, Charles University in Prague and in 1952 received his RNDr. degree based on a dissertation dealing with a detailed evaluation of the role of benthic macrofauna in three Lake backwaters. He started his scientific activities as a valuable member of a team of enthusiastic young limnologists gathered around his teacher J. Hrbáček.



He extended his interest in benthic fauna of small backwaters and oxbows to the wider field of fishponds and reservoirs and devoted special interest to a very difficult group of aquatic insects of the family Chironomidae (Diptera). In 1957 he received the CSc degree for his thesis dealing with the impact of the fish predation on benthic fauna. Starting in 1962, he was the head of the Department of Hydrobiology at the Faculty of Science until his retirement in 1991.

He lived the very active life of a university teacher, supervised more than seventy MSc and CSc theses and gave lectures in animal ecology, limnology and ecology of chironomid larvae. He was active in all aspects of academic life and served as the vice-dean for research and international affairs of the Faculty from 1974 to 1980. In those difficult times for the Czech scientific community, he was respected for his human and honest approach to all problems. His biological knowledge was encyclopedic and he was famous for his good memory for exact numbers. He was a devoted fan of scuba diving which he used to collect marine fauna for biological courses.

He was a founding member of the Czechoslovak Limnological Society serving as vice-president and later as the president in the late seventies. His activities covered other scientific societies as well: Czechoslovak Zoological Society, Czechoslovak Entomological Society, Czechoslovak Biological Society, section Ecology, International Limnological Society (SIL) and International Ecological Society (INTECOL). He presented his scientific results at many congresses, symposia and workshops. In appreciation of his activities, he was awarded the golden medal of the Faculty of Science and a diploma for merits in the development of Czech zoology. Due to his profound knowledge, he was able to organize a special symposium on

Chironomidae in 1976 in Prague. Between 1964 and 1974 he was active in the freshwater productivity field of research within the frame of the International Biological Programme.

Prof. Lellák published as the sole author or coauthor 20 books, handbooks and teaching texts for university students, and prepared identification keys for chironomid larvae and altogether published over 70 scientific papers. His interest was aimed during his entire professional life to benthic fauna. His original experiments with large cages covering the bottom of fishponds and protecting the fauna from fish predation or exposing it to various predatory pressure are famous among the students of limnology. He verified a hypothesis about the direct impact of fish predation on the biomass, abundance and species composition of bottom fauna and its relation to the changing intensity of the rain of particulate food from the overlying water column.

Prof. Lellák was very modest and human personality. He always tried to avoid conflicts, to find acceptable solutions to problems, and to deal with them and people involved in quiet and peaceful manner. He was respected and popular among his fellow limnologists and friends for his optimism and cheerful disposition. He will always be an inseparable part of the history of the development of our modern limnological research, and a fondly remembered person among his disciples and colleagues.

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